



NEW OBSERVATIONS AND REINTERPRETATION ON THE ENIGMATIC TAXON *COLOMBITHERIUM* (?PYROTHERIA, MAMMALIA) FROM COLOMBIA

by GUILLAUME BILLET*, MAËVA ORLIAC†, PIERRE-OLIVIER ANTOINE‡,§¶ and CARLOS JARAMILLO**

*IPHEP, CNRS UMR 6046, Faculté des Sciences Fondamentales et Appliquées, Université de Poitiers, 40, avenue du Recteur Pineau, 86022 POITIERS Cedex, France; e-mail guillaume.billet@univ-poitiers.fr

†Institut des Sciences de L'Evolution, CNRS UMR 5554, Université de Montpellier II – C.C. 064, Place Eugène Bataillon, F-34095 MONTPELLIER Cedex 5, France; e-mail maeva.orliac@univ-montp2.fr

‡Université de Toulouse; UPS (SVT-OMP); LMTG; 14 Avenue Édouard Belin, F-31400 Toulouse, France

§CNRS; LMTG; F-31400 Toulouse, France

¶IRD; LMTG; F-31400 Toulouse, France; e-mail poa@lmtg.obs-mip.fr

**Center for Tropical Paleocology and Archeology, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panama; e-mail jaramilloC@si.edu

Typescript received 21 April 2009; accepted in revised form 5 June 2009

Abstract: The controversial taxon *Colombitherium tolimense* (Mammalia) (probably Late Eocene in age) from Colombia, although known for nearly 40 years, still bears much mystery. Aside from the problematic ordinal attribution of the holotype and only specimen, its determination as an upper or lower jaw remains a highly debated issue. New observations include the presence of a contact facet on the distal face of the most posterior tooth, which indicates that the fragmentary jaw preserves three premolars and two molars; the M3, unrepresented but present, being most probably reduced. This new interpretation completely fits the morphology of the teeth. Furthermore, the shape of these latter and the deeper wear encompassed by their lingual part relative to the labial one is typical of upper dentition. This is in agreement with the internal curving of the roots of the anterior premolars and with several other arguments that lead interpreting the holotype of *C. tolimense* as a maxillary bearing P2-M2. This new interpretation deepens the morphological gap between

Colombitherium and other pyrotherians (except *Proticia*) and challenges further its referral to Pyrotheria. The peculiar morphology of *Colombitherium* relative to other pyrotherians is indeed striking. In fact, *Colombitherium* has nothing in common with pyrotherians but bilophodont cheek teeth, a feature largely widespread in placental mammals. It is here referred to ?Pyrotheria until additional evidence of its relationships is known. Associated with the putative removal of *Proticia* from Pyrotheria as argued by some authors, the hypothetical removal of *Colombitherium* from the order would adjust the widely accepted assumption that the pyrotherian bilophodont cheek teeth originated from bunodont cheek teeth. It would also make an origin from lophodont forms plausible. This in turn would have critical relevance, especially to the hypothesis that pyrotherians are notoungulates.

Key words: bilophodont, Eocene, maxillary, ungulate, anatomy, systematics.

ALTHOUGH *Colombitherium tolimense* Hoffstetter, 1970 from Colombia was described four decades ago, most about this puzzling mammal still bears much mystery. First, its stratigraphic origin and age remain vague: *Colombitherium* has been reported from an unnamed locality from the Gualanday Group in Colombia, supposedly Eocene in age (Hoffstetter 1970). Second, the highest doubt about this taxon comes from the nature of its holotype and only specimen MNHN-CLB 15, a fragmentary jaw bearing five bilophodont cheek teeth. In the original description, this jaw is

interpreted as a right maxillary with P3-M3 (Hoffstetter 1970; Kramarz and Bond 2005). On the contrary, some recent challengers defended the hypothesis of a left dentary with p3-m3 (Avilla 2005; Salas *et al.* 2006), and no agreement exists today on this issue. Actually, only the taxonomic referral of this taxon to Pyrotheria appears to be consensual (e.g. Hoffstetter 1970; Patterson 1977; McKenna 1980; Lucas 1986; Cifelli 1993; McKenna and Bell 1997; Salas *et al.* 2006), even though Hoffstetter (1970) conceded that this attribution was tentative as many differences exist between *Colombitherium* and

Pyrotheriidae. This is the reason why he erected the Colombitheriidae as a separate family. The Colombitheriidae currently include *Colombitherium* and *Proticia* Patterson, 1977, a controversial taxon from the Eocene or Miocene of Venezuela (Patterson 1977; McKenna and Bell 1997; Sánchez-Villagra *et al.* 2000). The Pyrotheriidae are based on *Pyrotherium* Gaudry, 1909, the only well-known pyrothere, from the Deseadan South American Land Mammal Age (SALMA; late Oligocene) of Patagonia and Bolivia (Gaudry 1909; Loomis 1914; MacFadden and Frailey 1984; Patterson 1977; Shockey and Anaya 2004). The Pyrotheriidae also include *Propyrotherium* Ameghino, 1901 from the Mustersan SALMA of Patagonia (Ameghino 1901; Simpson 1967), *Griphodon* Anthony, 1924 from the ?Eocene of Peru (Anthony 1924; Patterson 1942), *Baguatherium* Salas *et al.*, 2006, from the early Oligocene ('pre-Deseadan SALMA'), of Peru (Salas *et al.* 2006), and with some doubts *Carolozittelia* Ameghino, 1901 from the Eocene Casamayoran SALMA of Patagonia (Ameghino 1901; Simpson 1967).

We provide here a new interpretation based on original observations on the holotype of *C. tolimense*. This offers critical information for the taxonomic referral of *Colombitherium* and has relevance concerning the broader issue of the enigmatic origin of the Pyrotheria.

Institutional abbreviations: MNHN-CLB, Colombia collection, Muséum national d'Histoire naturelle, Paris, France.

SYSTEMATIC PALAEOONTOLOGY

EUTHERIA Gill, 1872

?PYROTHERIA Ameghino, 1895

Genus COLOMBITHERIUM Hoffstetter, 1970

Colombitherium tolimense Hoffstetter, 1970

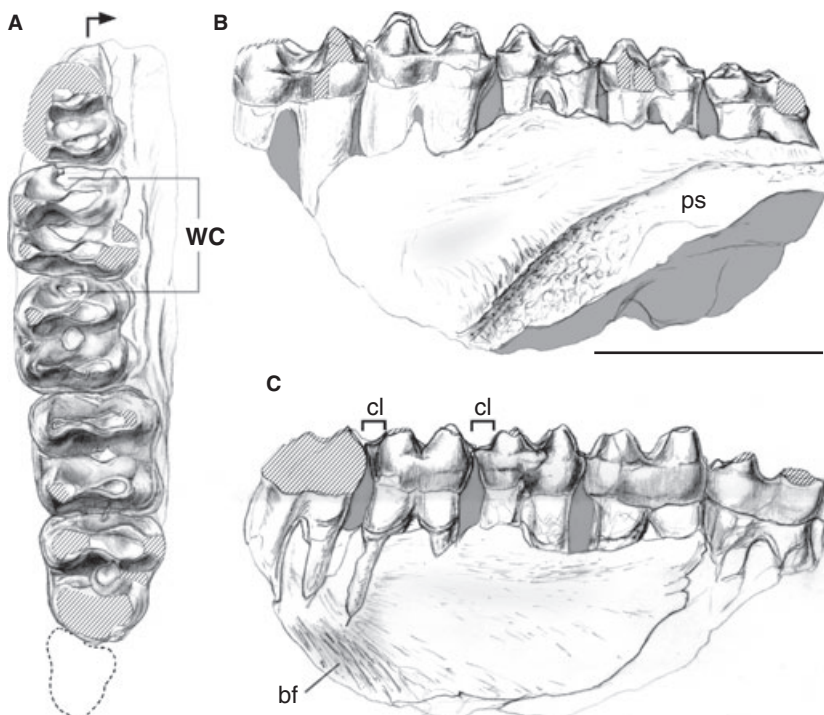
Text-figures 1–3

Holotype and only specimen. MNHN-CLB 15, a fragmentary right maxillary with P2–M2 (Text-fig. 1) according to the new interpretation presented in this study.

Occurrence. Lower part of the Gualanday Group (Late Eocene) of Colombia (Hoffstetter 1970; Santos *et al.* 2008; see discussion).

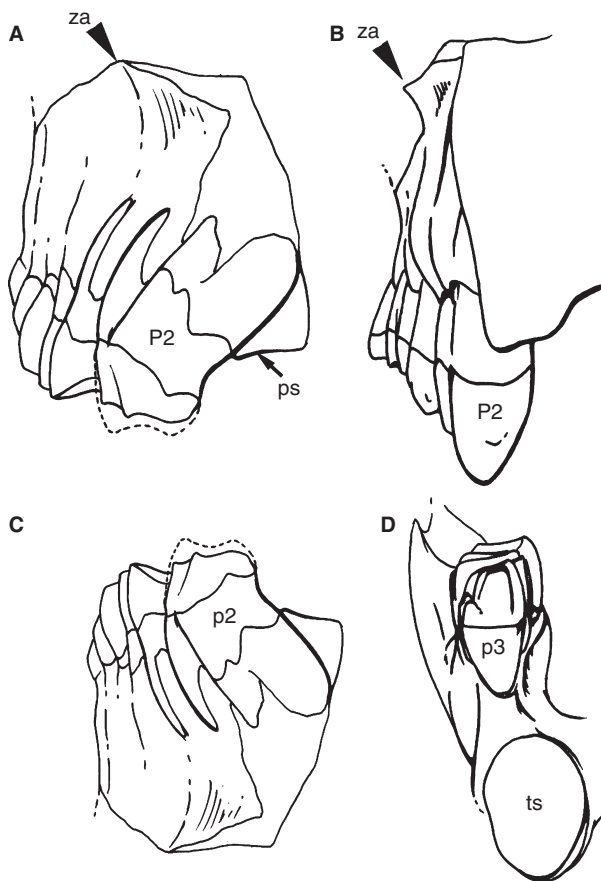
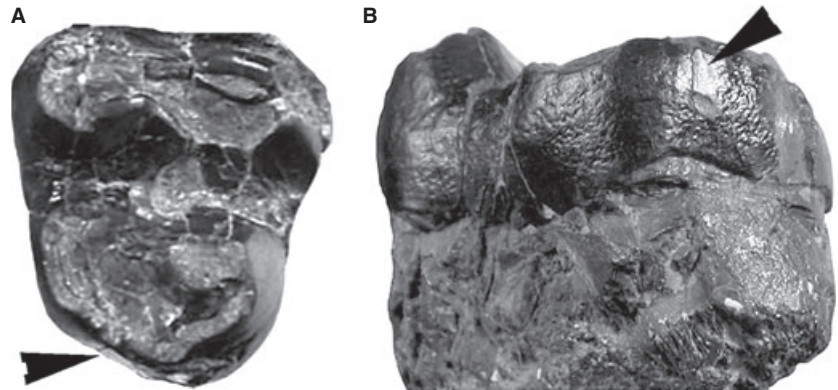
NEW OBSERVATIONS AND REINTERPRETATION OF MNHN-CLB 15

The fragmentary jaw MNHN-CLB 15 can be oriented thanks to an oblique bony process, c. 9-cm long, broken and located along one of the sides parallel to the tooth row. The side bearing this section shall be interpreted as the lingual one as this feature can only correspond to the broken part of either a symphysis or a palate. The opposed side is entirely smooth, without any process or foramen, which argues for a labial side. The broken bony



TEXT-FIG. 1. *Colombitherium tolimense*, holotype MNHN-CLB 15, partial right maxilla with P2–M2 (new interpretation) from the Late Eocene middle Gualanday of Colombia. A, occlusal view. B, lingual view. C, labial view. Hatched areas indicate damaged parts. Grey surfaces correspond to sediment filling still present on the specimen. Dotted lines indicate the putative outline of the M3. bf, frame of bone; cl, mesial cingulum ledge; ps, palatal section; wc, crucible wear facet. Scale-bar represents 5 cm.

TEXT-FIG. 2. *Colombitherium tolimense*, detail of the right M2 of the holotype MNHN-CLB 15. A, occlusal view. B, disto-labial view. The black arrow indicates the contact facet observable on the distal side of the M2.



TEXT-FIG. 3. Comparative schematic drawings of anterior views of the holotype of *Colombitherium tolimense* MNHN-CLB 15 and *Pyrotherium romeroi*. A, C. *tolimense* MNHN-CLB 15 represented according to the 'upper-jaw' hypothesis (privileged here). B, *P. romeroi*, MNHN-DES 1243, incomplete rostrum with right and left P2-M3. C, C. *tolimense* MNHN-CLB 15 represented according to the 'lower-jaw' hypothesis. D, *P. romeroi*, MNHN-DES 1238, subcomplete mandible with tushes (right broken) and right p3-m3 and left p3, m1-3. ps, palatal shelf; ts, tusk section; za, onset of zygomatic arch.

section located on the inferred lingual side is oblique and bow shaped. It presents one extremity lying at the level of the alveolar line, which is interpreted as anterior, and the other extremity running away, opposite to the occlusal plane. The tooth size is increasing backwards until the 4th cheek tooth, while the 5th and most posterior tooth tapers posteriorly (Text-fig. 1A).

The posteriormost tooth of the specimen presents a clear contact facet on its distal face, which was not mentioned in previous articles devoted to *Colombitherium* (Text-fig. 2; Hoffstetter 1970; Avilla 2005; Kramarz and Bond 2005; Salas *et al.* 2006). Obviously, this facet implies the presence of a distal tooth contiguous with the distalmost one preserved on MNHN-CLB 15. As a consequence and considering *a priori* there is no supernumerary tooth, the concerned specimen does not exhibit P3-M3 or p3-m3 (contra Hoffstetter 1970 and Salas *et al.* 2006), but rather P2-M2 or p2-m2. This new interpretation is fully congruent with the fact that what we interpret here as a fourth premolar – originally interpreted as a M1/m1 – is in fact (1) rigorously identical to the contiguous anterior tooth, i.e. the third premolar, and (2) presenting great differences with the two distalmost teeth of the specimen, which correspond to the first and second molars, respectively. Following this hypothesis, the third and fourth premolars are narrower labio-lingually than the first and second molars, the latter being more extended towards the lingual side. The first and second molars do not present the mesial ledge formed by the mesial cingulum (Text-fig. 1C), nor the mesial enamel crucible of wear (Text-fig. 1A) observed on premolars. The interpretation of the specimen MNHN-CLB 15 as a jaw with P2-M2 or p2-m2 is much more satisfactory with respect to the classical ungulate tooth Bauplan than previous hypotheses of a p3-m3 or P3-M3 series.

A difference of wear stages could also have been informative to determine the nature of the teeth present on MNHN-CLB 15, with M1/m1 bearing usually the most advanced wear stage, because of the tooth eruption sequence in placentals (Ziegler 1971; Slaughter *et al.* 1974; Martin

1997; Luo *et al.* 2004). However, no differences between the preserved teeth can be sorted out in this purpose.

This new interpretation is especially relevant for the long running debate about the nature of the jaw fragment MNHN-CLB 15. As described above, the molars show a greater labio-lingual diameter than premolars because of their larger lingual extent. This configuration is much more common on upper cheek teeth than on lower ones and would be an argument for interpreting MNHN-CLB 15 as a maxillary, following Hoffstetter (1970). Actually, several convincing arguments exist in favour of such an interpretation and are exposed in the following sections.

In tribosphenic therian mammals (Boreosphenida *sensu* Luo *et al.* 2001), the basin-like heel of lower molars (talonid) grinds (tribein) with the large inner cusp (protocone) on the upper molar and the wedge-like trigonid (sphen) shears with the crests of the corresponding upper tooth (Luo *et al.* 2001). These versatile occlusal functions in boreosphenidans are necessarily associated with lower molars more internal (lingual) than upper ones during occlusion. This generally produces deeper wear on the occluding lingual part of the upper cheek teeth and on the labial part of the lower ones than on other parts of these teeth. Therefore, in all boreosphenidans, upper cheek teeth tend to present higher relief on their labial side than on their lingual one, and consequently, the opposite case is observed on lower ones. Hence, the higher relief of the labial cusps in all cheek teeth on MNHN-CLB 15 strongly supports it as a maxillary, as already argued by Hoffstetter (1970) and Kramarz and Bond (2005). Comparison with other pyrotherians leads to the same conclusion. Indeed, late diverging pyrotherians such as *Pyrotherium* do not present any differential relief of the labial and lingual sides of their cheek teeth. However, in the late Eocene pyrotherian *Griphodon*, the lophids of the lower cheek teeth are lingually higher than labially (Patterson 1942). This demonstrates that the usual pattern of differential relief between upper and lower cheek teeth observed among boreosphenidans is also present in some early diverging pyrotherians. Besides, the slope observable on the lingual edge of molars of MNHN-CLB 15 also argues for the 'upper-jaw' hypothesis we stand for here.

The roots of P2–3 are made apparent by the fading away of the overlying bone (Text-fig. 1C). This latter is very thin in this area, a feature according well with a maxillary bone whose thin facial portion moulds premolar roots in most placentals and even sometimes breaks away to leave roots observable. The roots of P2–3 of *C. tolimense* present further evidence of the upper nature of these teeth. As far as can be seen, the anterior and posterior roots of P2 and at least the anterior one of P3 are clearly curved inward in a way that perfectly fits with the forward curving of the maxillary bone (Text-fig. 3A). This

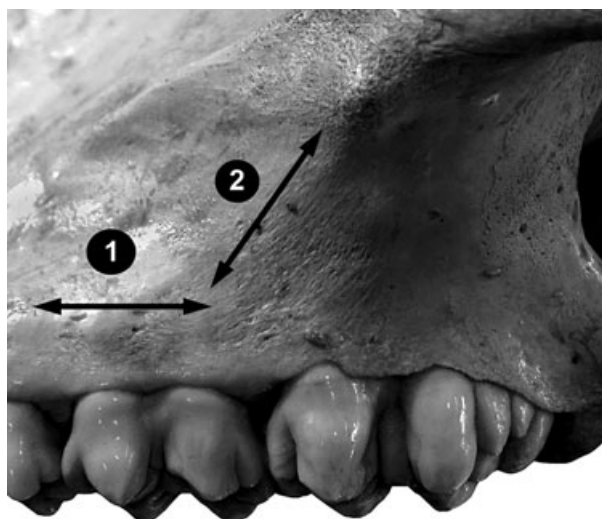
curving inward of premolar roots is also typical of upper teeth relative to lower.

Hoffstetter (1970) indicated that, at first glance, the bow-shaped bony section present on the lingual side evokes a mandible symphysis rather than a palatal fragment. However, remaining evidences led him to conclude that this specimen was an upper jaw representative of an animal with palatal bones and choanae located high and far anterior. Yet he conceded that this would imply a rather aberrant cranial architecture. The unusual shape of this putative palate and its better *a priori* correspondence to a mandible have been used in some subsequent works as an argument in favour of the 'lower-jaw' hypothesis (Avilla 2005; Salas *et al.* 2006). However, we argue here that if MNHN-CLB 15 was a fragment of lower jaw, the morphology of the body of the mandible and of the symphysis would have been at least as 'aberrant' as if the specimen is regarded as a putative palate. The most posterior extremity of the bow-shaped bony section (mark of the symphysis in the 'lower-jaw' hypothesis) is not preserved (Text-fig. 1B). In other words, if a section of the symphysis, this latter would have extended at least as far back as the level of m1 and possibly more posteriorly to it; this would constitute a mandible with a strikingly huge symphysis. In *Pyrotherium*, the posterior tip of the symphysis is located below the p4-m1 limit. Moreover, the antero-posterior symphyseal profile in *Pyrotherium* is oblique and straight, and then clearly differs from the bow shaped one observed in *Colombitherium*.

Furthermore, a bony shelf located lingual to P2 is present on MNHN-CLB 15. It reaches the level of the alveolar line (Text-fig. 3A, C). This horizontal surface in the lingual vicinity of the second premolar fits much better with a maxillary palatal surface than with a symphysis (Text-fig. 3A, C, palatal shelf), especially when compared to *Pyrotherium* (Text-fig. 3B, D). Indeed, the mandible of this latter does not exhibit such a horizontal bony surface lingual to p2 (Text-fig. 3D). Besides, the symphysis of *Pyrotherium* is deeply excavated and presents a U-shaped transverse profile (Text-fig. 3D). Kramarz and Bond (2005) already pointed out that this shelf in *Colombitherium* was incompatible with a true symphysis.

The labial face of the jaw MNHN-CLB 15 is slightly sloping laterally, in the direction opposite to the occlusal plane. This lateral sloping may correspond to the onset of the zygomatic arch. Neither foramen nor canal can be detected on MNHN-CLB 15. It is conceivable that the facial opening of the infra-orbital foramen would have opened more dorsally than the portion of the maxilla preserved on the specimen.

The frame of the bone is detectable by tiny parallel lines regularly marked on the labial face of MNHN-CLB 15 (Text-fig. 1C). Oppositely to the framed bone observed on a mandible (parallel to the occlusal plane), these lines



TEXT-FIG. 4. Detail of the facial portion of the maxillary near the anterior root of the zygomatic arch, in the extant wild boar *Sus scrofa*. Arrow 1 indicates frame bone marked by horizontal lines, arrow 2 indicates frame bone marked by oblique lines.

orientate obliquely in the part adjacent to the premolars with an angle of 45° relative to the occlusal plane. Actually, the distribution pattern of these lines is characteristic of the onset of the maxillary root of the zygomatic arch, as can be seen for instance in the extant wild boar (Text-fig. 4, arrow 2). In the remaining distal part of this face, these lines are oriented more parallel to the occlusal plane (Text-fig. 4, arrow 1).

Finally, the combination of all the arguments exposed above strongly favours the ‘upper-jaw’ hypothesis and undoubtedly discards the ‘lower-jaw’ one. Therefore, MNHN-CLB 15 is interpreted as a right maxillary bearing P2-M2.

The missing M3 must have been reduced relative to other teeth as indicated by the small and unique contact facet observed on the latero-distal edge of M2 (Text-fig. 2), especially given that M2 is somewhat smaller than M1 and tapers backwards (i.e., the metaloph is narrower than the protoloph). In fact, it can be reasonably hypothesized that the M3 may have resembled a minor version of the M2, with a similar triangular occlusal outline (Text-fig. 1A).

DISCUSSION

Taxonomic referral of MNHN-CLB 15

Until now, *Colombitherium tolimense* has always been referred to the Pyrotheria (e.g. Hoffstetter 1970; Patterson 1977; Cifelli 1993; McKenna and Bell 1997; Salas *et al.* 2006), independently from the nature of its interpretation

(maxillary or dentary). Hoffstetter (1970) yet pointed out some striking differences between *Colombitherium* and *Pyrotherium*. He noted, among others, the retention of P2 in *Pyrotherium* but not in *Colombitherium* as a major difference. The new interpretation provided here invalids this difference, as P2 is actually present in *Colombitherium*. However, many other differences previously noted still subsist. Most of the characters unique to pyrotherians are absent in *Colombitherium*: wrinkled enamel, fully lophodont cheek teeth with indistinct cusps, crenulated cingulae and crests (Hoffstetter 1970). In the meantime, *Colombitherium* exhibits unique features absent in pyrotherians, which indicate a very original morphology: the deep palatal excavation and the dental wear characterized notably by a crucible wear facet in the valleys between lophs. Particularly, the deep and anterior palatal excavation is striking. This implies a very high opening of the choanae, far anterior in the skull, which, beyond its puzzling aspect, evokes a highly specialized anatomy.

Our new interpretation deepens the morphological gap between *Colombitherium* and pyrotherians. The presence in *Colombitherium* of an oblique lingual face on M2 is associated with the weak development of the distal loph (Text-fig. 1A). This clearly differs from other pyrotherians whose M2 is strictly squared, with a distal loph equal to the mesial one. Moreover, as argued above, the M3 of *Colombitherium* must have been reduced and triangular which further differentiates this taxon from other pyrotherians, with squared and unreduced M3; it is even the largest tooth of the series with M2 in pyrotherians.

It is also worth noting that the orientation of the labial roots of P2 are strongly curved inward in *Colombitherium* and rather straight in other pyrotherians, which is another difference between both taxa (Text-fig. 3A, B).

Hence, there are many differences between *Colombitherium* and other pyrotherians – this comparison does not include *Proticia*, whose referral to Pyrotheria is also highly controversial (Sánchez-Villagra *et al.* 2000). In fact, *Colombitherium* has nothing in common with pyrotherians but bilophodont cheek teeth, a feature largely widespread in placental mammals. This feature is also present in the Xenungulata, a Palaeocene group of South American endemic ungulates unrelated to Pyrotheria (Paula Couto 1952; Cifelli 1993; Shockey and Anaya 2004). Actually, the development or acquisition of bilophodonty presents much convergence in placental mammals, both intra-ordinally (e.g. *Barytherium/Numidothorium/Deinotherium* within Proboscidea (Delmer *et al.* 2006); tapirs and paleotheres within Perissodactyla (Cuvier 1822)) and inter-ordinally (xenungulates, perissodactyls, suid artiodactyls, pyrotherians, proboscideans, coryphodontid pantodonts, dinoceratans). The referral of *Colombitherium* to Pyrotheria is therefore weakly supported, and it must be considered as highly hypothetical. However, according to our

current knowledge of *Colombitherium*, this genus does not appear to fit better within any other placental order (except perhaps Tethytheria?). Hence, we recommend to refer *Colombitherium* to ‘Pyrotheria’, until additional evidence of its phylogenetic affinities has been encountered.

The age of Colombitherium

The middle Gualanday in the Gualanday area, where *Colombitherium tolimense* was found, has been poorly dated. A pollen sample from the upper part of the middle Gualanday indicates an age of Late Eocene to Oligocene (Pollen zones T07 to T-11 of Jaramillo *et al.* 2009) based on the presence of *Verrucatosporites usmensis* and *Cicatricosisporites* reported by Porta and Porta (1962). The last occurrence of *Echitriporites trianguliformis orbicularis* from the Gualanday formation in the Gigante area (about 150 km south) indicates that the upper part of the Gualanday formation contains the Eocene/Oligocene boundary – boundary between pollen zones T07 and T08 of Jaramillo *et al.* (2009). This upper segment also has marine influence (Santos *et al.* 2008). Therefore, a tentative correlation would suggest that the middle Gualanday in the Gualanday area is most probably Late Eocene in age.

CONCLUSION

According to our new observations, the holotype of *Colombitherium tolimense* (MNHN-CLB 15), which is tentatively referred here to the Late Eocene, is a right maxillary bearing P2-M2. This new interpretation deepens the morphological gap between *Colombitherium* and other pyrotherians (except *Proticia*) and challenges further its referral to Pyrotheria. This new issue provides new insights into pyrotherian origins. Associated with the putative removal of *Proticia* from Pyrotheria as argued by Sánchez-Villagra *et al.* (2000), the hypothetical removal of *Colombitherium* from the order would adjust the widely accepted assumption that the pyrotherian bilophodont cheek teeth originated from bunodont cheek teeth. It would also make it plausible an origin from lophodont forms. This in turn would have critical relevance especially on the hypothesis that considers pyrotherians as notoungulates (Patterson 1977; Billet 2008, 2009); this latter group containing exclusively lophodont forms. Therefore, in a roundabout way, these new considerations on *Colombitherium* and its dubious referral to Pyrotheria raise major issues about the relationships between Pyrotheria and Notoungulata. It allows more hypotheses about the enigmatic origins of the South American endemic Pyrotheria.

Acknowledgements. We thank Claire Sagne and Pascal Tassy from the *Muséum National d’Histoire naturelle* in Paris for kindly granting access to MNHN South American fossil mammals’ collection under their care. Many thanks to Manuel Martínez Cáceres (MNHN, Paris) for all its friendly help during the collections study in the MNHN. Thanks are also due to Rodolfo Salas Gismondi (MUSM, Lima) and Christian de Muizon (MNHN, Paris) for fruitful discussions about *Colombitherium*. We also acknowledge Darin Croft and Mariano Bond for their review of the paper.

Editor. Ruta Marcello

REFERENCES

- AMEGHINO, F. 1895. Première contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino*, **15**, 1–60.
- 1901. Notices préliminaires sur des ongulés nouveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional Ciencias de Córdoba, Buenos Aires*, **16**, 350–426.
- ANTHONY, H. E. 1924. A new fossil perissodactyl from Peru. *American Museum Novitates*, **111**, 1–13.
- AVILLA, L. S. 2005. A revision of *Colombitherium tolimense* Hoffstetter (Pyrotheria: Mammalia) and its significance on Pyrotheria relationships. *Ameghiniana*, **42**(4R), 60R.
- BILLET, G. 2008. *La faune de notongulés (Mammalia) de l’Oligocène supérieur de Salla (Bolivie) : phylogénie et affinités d’un groupe d’ongulés endémiques du Tertiaire d’Amérique du Sud*. Unpublished PhD dissertation, Muséum national d’Histoire naturelle, Paris, 430 pp.
- 2009. New observations on the skull of *Pyrotherium* (Pyrotheria, Mammalia) and new phylogenetic hypotheses on South American ungulates. *Journal of Mammalian Evolution*, doi: 10.1007/s10914-009-9123-0.
- CIFELLI, R. L. 1993. The Phylogeny of the Native South American Ungulates. 195–216. In SZALAY, F. S., NOVA-CEK, M. J. and MCKENNA, M. C. (eds). *Mammal Phylogeny, Volume 2: Placentals*. Springer Verlag, New York, 601 pp.
- CUVIER, G. 1822. *Recherches sur les ossements fossiles*, Vol. 3. Edmond d’Ocagne (ed.), Paris, 435 pp.
- DELMER, C., MAHBOUBI, M., TABUCE, R. and TASSY, P. 2006. A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria: new perspectives on the ancestral morphotype of the genus. *Palaeontology*, **49**, 421–434.
- GAUDRY, A. 1909. Fossiles de Patagonie: le *Pyrotherium*. *Annales de Paléontologie*, **4**, 1–28.
- GILL, T. 1872. Arrangement of the families of mammals and synoptical table of the characters of the subdivisions of mammals. *Smithsonian Miscellaneous Collections*, **11**, 1–98.
- HOFFSTETTER, R. 1970. *Colombitherium tolimense* pyrotherien nouveau de la Formation Gualanday (Colombie). *Annales de Paléontologie*, **56**, 149–171.
- JARAMILLO, C., RUEDA, M., BAYONA, G., SANTOS, C., FLOREZ, P. and PARRA, F. 2009. Biostratigraphy breaking paradigms: dating the Mirador Formation in the Llanos Basin of Colombia, 29–40. In DEMCHUK, T. and

- WASZCZAK, R. (eds). *Geologic problem solving with microfossils*. SEPM Special Publication 93, 342 pp.
- KRAMARZ, A. and BOND, M. 2005. Criticisms to the re-interpretation of the holotype of *Colombitherium tolimense* Hoffstetter (Mammalia: Pyrotheria) and its implication on the Pyrotheria – Notoungulata relationships. *Ameghiniana*, **42**(4R), 16R.
- LOOMIS, F. B. 1914. *The Deseado formation of Patagonia*. Rumford Press, Concord, Massachusetts, 232 pp.
- LUCAS, S. G. 1986. Pyrothere systematics and a caribbean route for land-mammal dispersal during the Paleocene. *Revista Geológica de America Central*, **5**, 1–35.
- LUO, Z. X., CIFELLI, R. L. and KIELAN-JAWOROWSKA, Z. 2001. Dual origin of tribosphenic mammals. *Nature*, **409**, 53–57.
- KIELAN-JAWOROWSKA, Z. and CIFELLI, R. L. 2004. Evolution of dental replacement in mammals. *Bulletin of Carnegie Museum of Natural History*, **36**, 159–175.
- MARTIN, T. 1997. Tooth Replacement in Late Jurassic Dryolestidae (Eupantotheria, Mammalia). *Journal of Mammalian Evolution*, **4**, 1–18.
- MCKENNA, M. C. 1980. Early history and biogeography of South America's extinct land mammals. 43–77. In CIOCHON, R. L. and CHIARELLI, A. B. (eds). *Evolutionary biology of the New World monkeys and continental drift*. Plenum Press, New York, 528 pp.
- and BELL, S. 1997. *Classification of mammals above the species level*. Columbia University Press, New York, 631 pp.
- MACFADDEN, B. J. and FRAILEY, C. D. 1984. *Pyrotherium*, a large enigmatic ungulate (Mammalia, incertae sedis) from the Deseadan (Oligocene) of Salla, Bolivia. *Palaeontology*, **27**, 867–874.
- PATTERSON, B. 1942. Two Tertiary mammals from northern South America. *American Museum Novitates*, **1173**, 1–7.
- 1977. A primitive pyrothere (Mammalia, Notoungulata) from the Early tertiary of Northwestern Venezuela. *Fieldiana Geology, N.S.*, **33**, 397–421.
- PAULA COUTO, C. de 1952. Fossil mammals from the beginning of the Cenozoic in Brazil: Condylarthra, Litopterna, Xenungulata and Astrapotheria. *Bulletin of the American Museum of Natural History*, **99**, 355–394.
- PORTA, J. and PORTA, N. Sole de. 1962. Discusion sobre las edades de las formaciones Hoyón, Gualanday y la Cira en la region de Honda-San Juan de Rioseco (Valle del Magdalena). *Boletín de Geología, Universidad Industrial de Santander*, **9**, 69–85.
- SALAS, R., SÁNCHEZ, J. and CHACALTANA, C. 2006. A new Pre-Deseadan Pyrothere (Mammalia) from northern Peru and the wear facets of molariform teeth of Pyrotheria. *Journal of Vertebrate Paleontology*, **26**, 760–769.
- SÁNCHEZ-VILLAGRA, M. R., BURNHAM, R. J., CAMPBELL, D. C., FELDMANN, R. M., GAFFNEY, E. S., KAY, R. F., LOZSÁN, R., PURDY, R. and THEWISSEN, J. G. M. 2000. A new near-shore marine fauna and flora from the Early Neogene of Northwestern Venezuela. *Journal of Paleontology*, **74**, 957–968.
- SANTOS, C., JARAMILLO, C., BAYONA, G., RUEDA, M. and TORRES, V. 2008. Late Eocene marine incursion in north-western South America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **264**, 140–146.
- SHOCKEY, B. J. and ANAYA, F. 2004. *Pyrotherium macfaddeni*, sp. nov. (late Oligocene, Bolivia) and the pedal morphology of pyrotheres. *Journal of Vertebrate Paleontology*, **24**, 481–488.
- SIMPSON, G. G. 1967. The beginning of the age of mammals in South America, Part 2. *Bulletin of the American Museum of Natural History*, **137**, 1–259.
- SLAUGHTER, B. H., PINE, R. H. and PINE, N. Etoh. 1974. Eruption of cheek teeth in Insectivora and Carnivora. *Journal of Mammalogy*, **55**, 115–125.
- ZIEGLER, A. C. 1971. A Theory of the Evolution of Therian Dental Formulas and Replacement Patterns. *The Quarterly Review of Biology*, **46**, 226–249.