Journal of Systematic Palaeontology **4** (3): 279–284
doi:10.1017/S1477201906001830 Printed in the United Kingdom
Issued 11 August 2006

A new Megadolodinae (Mammalia, Litopterna, Protherotheriidae) from the Urumaco Formation (Late Miocene) of Venezuela

Alfredo A. Carlini
Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n B1900FWA La Plata, Argentina and CONICET, Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina

Javier N. Gelfo
Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina and CONICET

Rodolfo Sánchez
Museo Paleontológico de la Alcaldía de Urumaco, Falcón, Venezuela

SYNOPSIS A new genus and species of Proterotheriidae Megadolodinae, *Bounodus enigmaticus*, from the Upper Miocene Urumaco Formation of Venezuela, is described on the basis of a poorly preserved right maxillary fragment with brachydont cheek teeth. Teeth and alveoli preserved are interpreted as part of the alveolus of P3 and P4–M3. The new taxon differs from *Megadolodus*, the only other known genus of the subfamily, in having a proportionally smaller P4 and M1, the latter elongated antero-posteriorly and with the protocone root more mesial than that of the hypocone. *Bounodus enigmaticus* gen. et sp. nov., reinforces the hypothesis that the Megadolodinae represent a distinct radiation within the Proterotheriidae, the two other major clades being the Anisolambdinae and Proterotheriinae.

KEY WORDS *Bounodus enigmaticus*, native ungulates, Miocene, Tertiary, South America

Contents

Introduction

The Litopterna, which first appear in the Palaeocene (Peligran age) of Patagonia (Bonaparte & Morales 1997), were the second most successful and diverse Tertiary ungulates in South America surpassed only by the Notoungulata. There is currently no consensus about their higher-level taxonomy, but it is agreed that the following clades belong to it: Macraucheniidae, Proterotheriidae, Adianthidae and Notonychopidae. Sparnotheriodontidae were classified as 'Condylarthra' by Cifelli (1983*a*,*b*), based upon the assumed association of tarsal and dental remains. However, this was not followed by Soria (2001), who argued that Sparnotheriodontidae belonged within the Litopterna.

In contrast to notoungulate contemporaries with their more hypsodont teeth, most litopterns retained a low-crowned dentition which presumably was not well suited to the increasingly dry, open savannas that started to develop in the middle part of the Tertiary and subsequently came to dominate, at least in middle to high latitudes. In

consequence, the distribution, diversification and extinction of litopterns are usually attributed to changing environmental conditions (Cifelli & Guerrero 1997).

Only a few South American native 'ungulates' have so far been reported from the Urumaco Formation (late Miocene) of Venezuela, all attributed to the Toxodontidae (Aguilera 2004). Recently Linares (2004) listed various other autochthonous genera (e.g. *Hemihegetotherium*, *Protypotherium*) but described and illustrated only the Toxodontidae (*Gyrinodon* Hopwood, 1928 and *Ocnerotherium* Pascual, 1954, *sic*). McKenna (1956) described *Megadolodus molariformis* and assigned this strange taxon to the 'condylarthra' Didolodontidae, a basal South American clade of mammals, on the basis of the very bunodont structure of its dentition. Cifelli & Villarroel (1997) analysed the affinities of *M. molariformis* and, based upon postcranial remains, deduced that it is not a 'primitive condylarth' but a low latitude group of Litopterna Proterotheriidae, distinct from the typically Patagonian lineages already known. *Megadolodus molariformis* was collected from the middle Miocene sediments of La Venta, Colombia, together with other Litopterna Proterotheriidae and Macraucheniidae known exclusively from this locality, and compared with the known records of litopterns of higher latitudes (Cifelli & Guerrero 1997). In this paper, a new genus and species of Megadolodinae from the Urumaco Formation, Venezuela, is reported. It is the second megadolodine to be described, broadening the geographical and stratigraphical distribution of the subfamily and reinforcing the idea of a low latitude 'endemic' subfamily.

Institutional abbreviations

AMU-CURS, Collection of Vertebrate Palaeontology of the Alcaldía de Urumaco, Estado Falcón, Venezuela.
IGM, Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Museo Geológico, Bogotá, Colombia.
MACN, Collection of Vertebrate Palaeontology, Museo Argentino de Ciencias Naturales, 'Bernardino Rivadavia', Buenos Aires, Argentina.
MLP, Collection of Vertebrate Palaeontology, Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina.

Systematic Palaeontology

LITOPTERNA Ameghino, 1889
PROTEROTHERIIDAE Ameghino, 1887
MEGADOLODINAE Cifelli & Villarroel, 1997
BOUNODUS gen nov.

ETYMOLOGY. *'Bouno'* from the Greek βουνο, which means hill, for the morphology of the teeth cusps and '*odus*' from the Greek οδυσ for tooth.

TYPE SPECIES. *Bounodus enigmaticus* gen. et sp. nov.

REFERRED SPECIES. Only the type species.

OCCURRENCE. Urumaco, Estado Falcón, Venezuela; Upper Member of the Urumaco Formation, late Miocene (Aguilera 2004; Ministerio de Energía y Minas 1997).

DIAGNOSIS. Differs from *Megadolodus* McKenna 1956, in having a proportionally smaller P4 and M1, the latter elongated antero-posteriorly and with the protocone root more mesial than that of the hypocone.

Bounodus enigmaticus sp. nov. (Fig. 1)

ETYMOLOGY. '*Enigmaticus*' according with its peculiar morphology, uncommon among litopterns.

HOLOTYPE. AMU-CURS 44, fragment of right maxilla, with P4–M3 and the alveolus of the P3, part of the maxillar lateral wall and palatal roof. No other specimens known.

OCCURRENCE. As for genus.

DIAGNOSIS. As for genus.

DESCRIPTION. AMU-CURS 44 is a right maxillary fragment poorly preserved, with brachydont cheek teeth, interpreted as part of the alveolus of P3, and P4–M3 (Figs 1A–C). The fossil shows part of the labial side of the maxillar bone broken to expose some of the roots. At the position of the P3, an anterior remnant of a root alveolus descends anterolabially and seems to be divided by a straight central crest. The posterior wall of the alveolus shows two parallel roots, a lingual one and a deeply labial one. This condition results in a triangular P3 outline with the major axis projected antero-posteriorly. The first tooth remnant interpreted as P4 is triangular, with a main antero-posterior axis. The inferred outline of the tooth can be compared with dP3 of *Megadolodus molariformis* (IGM 18382) as being posteriorly wider and anteriorly sharp. The tooth is badly preserved and the labial portion is particularly damaged. The enamel, dentine and almost all of the roots have been destroyed, leaving only the upper portion of the roots in occlusal view and an empty alveolus. Only the more posterior portion of the anterior root is present, but the size of the alveolus suggests it was a large structure. The posterolingual root is more lingual than the anterior one and is positioned almost at the same transverse line with respect to the labial one. Little can be inferred about the cusps. Neither the parastyle nor the cristids or enamel folds could be discerned. The paracone seems to have been placed in a very anterior position and probably was the principal cusp (Figs 1D & E). The M1 (length 13.26 mm antero–posterior by and width 12.28 mm labio–lingually) is better preserved (Fig. 1) and, although the lingual and labial sides are broken, a square outline can be inferred. In contrast to the M2 the major axis is antero–posterior. The posterior side of the tooth is transversely wider than the anterior side. Four roots are present, those that support the protocone and the anterolabial below the paracone being close together. The posterior labial and lingual roots (larger) are related to the metacone and hypocone, respectively. The protocone and hypocone are subequal in size, with the apices close together. But a remnant of enamel extends from the lingual base of the protocone to the hypocone, suggesting that the base of the latter was more lingually expanded. The enamel of the posterolingual side of the hypocone is broken, leaving a soft dentine surface. In contrast to most Didolodontidae and Litopterna, the hypocone is not associated to a strong posterior cingulum but only to a thin posterior rim. No conspicuous anterior cingulum seems to be present. A small and rounded metaconule contacts the labial border of the hypocone and contacts also the lingual side of the worn metacone. Even

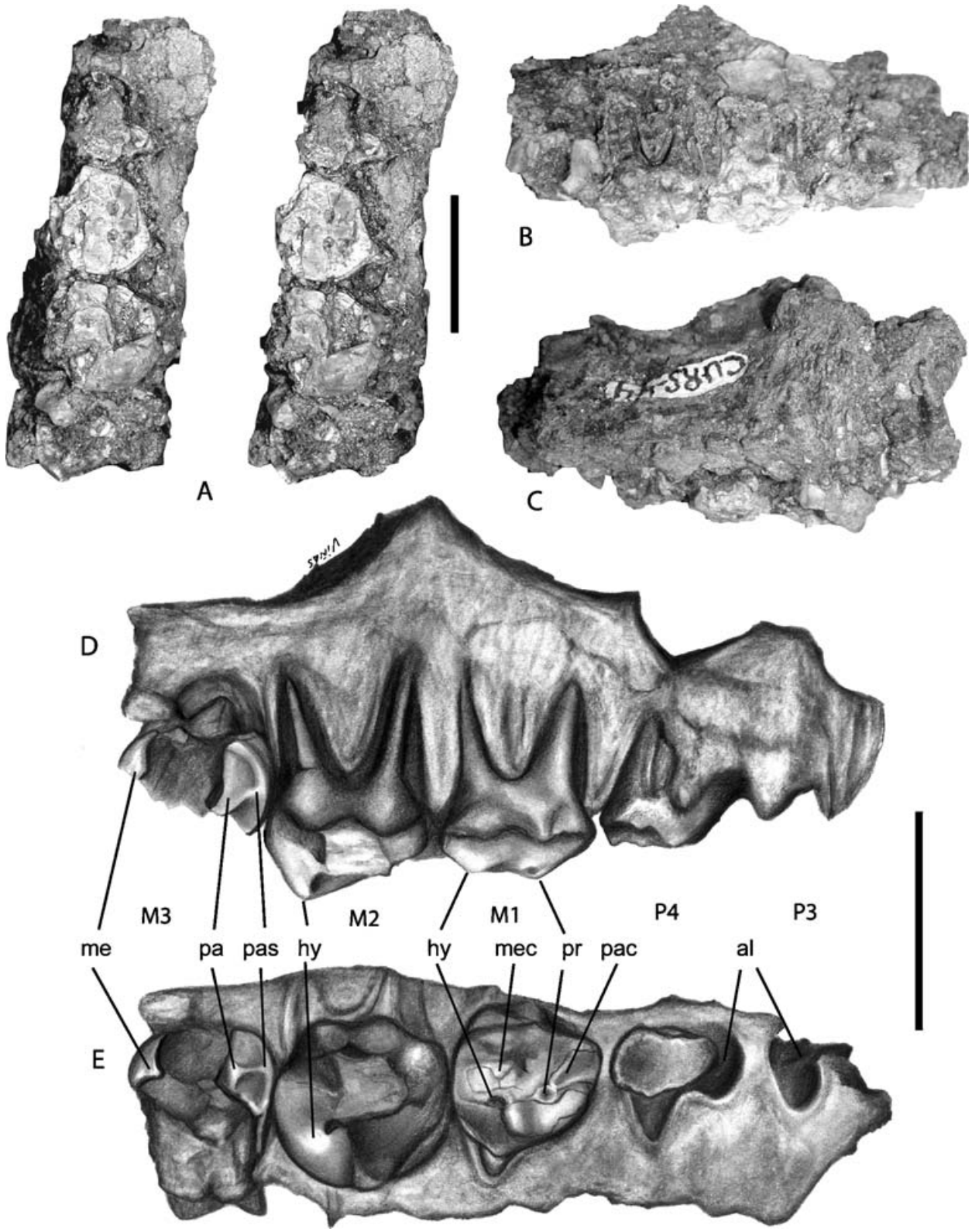

Figure 1 *Bounodus enigmaticus* gen. et sp. nov. AMU-CURS 44, holotype. Fragment of right maxillar. **A**, stereo pair in occlusal view; **B**, labial view; **C**, lingual view; **D**, drawing in lateral view; **E**, drawing in occlusal view. Abbreviations: **al**, alveolus; **hy**, hypocone; **M**, upper molars; **me**, metacone; **mec**, metacrista; **pa**, paracone; **pac**, paracrista; **pas**, parastyle; **pr**, protocone; **P**, upper premolars. Scale bar = 2 cm.

though the region of the post metaconular crista is broken, the outline of the metaconule suggests it was absent. The paraconule of M1 has been erased by wear, but a wide dentine surface extends from the anterior broken enamel border of the protocone through the anterolabial side of the tooth. In contrast to the metaconule, which is located in the same line as the hypocone, the paraconule seems to be located much more anteriorly than the protocone. The presence or absence of the paraconule crista could not be established. Despite the anterior position of the paraconule, the bulbous base of the metaconule delimits a short trigon basin. The labial side of the tooth is broken, consequently, only the internal border of the paracone and metacone are present. The M2 (length 13.52 mm antero-posterior by and width 14.34 mm labio-lingually) is also very broken (Fig. 1), square in outline with predominantly a labio-lingual diameter. The protocone is almost destroyed except for a faint portion of enamel that overlaps the anterior side of the hypocone. The protocone seems to be proportionally larger than the hypocone and a little more lingually settled, but little else could be inferred about it. In contrast to M1, the hypocone shows no wear, except for showing a very slight dentine surface, which runs anterior from the apex of the cusp, towards where the labial side of the protocone should be placed. Even though there is no strong posterior cingulum, the posteriolabial portion of the hypocone seems to be connected to a faint rim. The labial side of the tooth has no trace of the paracone and metacone. The exact position of the metaconule could not be inferred, but for the little enamel preserved in the trigon area, it seems to be located more anteriorly than the hypocone, in contrast to the situation described for M1. The paraconule is anteriorly placed and associated with a strong preparaconular crista, which projects anterolabially. Compared with the sparse wear of the hypocone, the paraconule shows precocious wear, which could in fact explain the erased paraconule of M1. The M3 (length 12.68 mm antero-posterior by and width 16.22 mm labio-lingually) seems not to be fully erupted (Fig. 1) and is buco-lingually larger than M2. The only preserved parts of this tooth are the paracone and the anterolabial side of the paraconule. What seems to be a short preparaconular crista, contacts the faint anterior by cingulum (Figs 1D & E). The preparacrista is straight and contacts the anterior cingulum at 90°, at the small parastyle. The anterolabial side of M3 shows the reduction of the cingulum, which we infer was absent on the labial margin of the paracone. The other enamel remnant is the base of the posterolabial side of the metacone. According to the development of the postero-labial root, a strong hypocone is inferred.

Discussion

The shape of the molars of *Bounodus* is similar to that of the Didolodontidae condylarths, a clade endemic to South America and apparently restricted to the Palaeogene. In fact, the majority of younger taxa once referred to this family on the basis of tooth characters are now considered to be litopterns when postcranial remains are known. This is the case of *Megadolodus*, to which the taxon described here is most closely related, and *Neodolodus colombianus* Hoffstetter & Soria, 1986, from the Miocene of Colombia. However, the latter was considered to be a junior synonym of *Prothoatherium* Ameghino, 1902 by Cifelli & Guerrero Diaz (1989: but see Soria 2001). *Prothoatherium colombianus* shares with *Bounodus* the absence of strongly lophate cheek teeth, but differs from it in the general shape and minor size of the molars, the broadly developed anterior cingulum on the lingual base of the protocone and the lingual sulcus that separates the protocone and hypocone. Another taxon, *Salladolodus deuterotheroides* Soria & Hoffstetter, 1983, from the Deseadan (Lower Oligocene) of Bolivia, known from a left M2–3 and considered to be a Didolodontidae (Soria & Hoffstetter 1983), differs from *Bounodus* in its somewhat smaller size, the peculiar absence of metaconule and the continuity between hypocone and posterior cingulum. *Bounodus* recalls particularly the large-sized Didolodontidae, such as *Paulogervaisia mamma* Ameghino, 1901, from the Casamayoran (probably Barrancan) of Patagonia. Although this taxon is known only from fragmentary remains it seems valid (Simpson 1948; Cifelli 1983*a*; Soria 2001) and not a synonym of *Didolodus* Ameghino, 1897 (*contra* McKenna & Bell 1997). *Paulogervaisia* Ameghino, 1901 (MACN 10719) differs from *Bounodus* in having M3 with a more rounded contour and smaller in size compared to M2; the more lingually placed hypocone and the separation of this cusp with respect to the protocone. The size inferred for *Bounodus* based on the inferred P4 suggests it had a greater degree of molarisation than did Didolodontidae. This is observed among the Proterotheriidae Megadolodinae. In this sense, *Bounodus* shares with *Megadolodus molariformis* the presence of a bunodont dentition, hypocone in M3 and the very anterior position of the paraconule that tends to interrupt the trajectory of the anterior cingulid. However, it differs by having a rectangular contour of M1 with a more mesial antero-lingual root. In addition, the anterior border of the hypocone in M2 shows a lingual margin of enamel interpreted as the most posterior portion of the protocone; consequently, the hypocone would be more labial with respect to the protocone in *Bounodus* rather than posterior as in *Megadolodus*.

Bounodus enigmaticus represents a new genus and species that reinforces the idea that the poorly known Megadolodinae represent a lineage developed independently from the rest of the Proterotheridae represented by the Anisolambdinae and Proterotheriinae, *sensu* Cifelli (1983*a*). The Anisolambdinae were diagnosed by the presence of molariform crown of intermediate height and well-developed paralophids ending in a large paraconid (Cifelli 1983*a*). Some of the taxa included in this group were recognised as the Anisolambdidae (Soria 2001). Some species included in this group are known only by part of the dentition, but are comparable to the material described here. *Xesmodon langi* (Roth 1899: MLP 12-1481) from the Mustersan of Patagonia has been referred to both the Didolodontidae and the Proterotheriidae (Simpson 1948; Odreman Rivas 1969; Soria 2001). *Bounodus* shares with *Xesmodon* Berg, 1899, a strong hypocone in M3 (inferred for the former), the anterior location of the metaconule (a character also seen in *Megadolodus*) and the strong labially projected preparaconular crista, which in *Xesmodon* joins in the parastyle with the reduced anterior cingulum and the preparacrista. However *Xesmodon* differs from *Bounodus* in having a robust postcingulum that contacts the hypocone of M2. Furthermore, the slightly crenulate or undulate enamel of *Xesmodon* recalls the rugosities of the enamel of *Megadolodus*. Other interesting characters in the M3 of *Xesmodon langi*, such as the short postmetaconular crista not reaching the metastyle and the development of the posterior

cingulum and robust postmetacrista, or absence of labial cingulum, cannot be compared with *Bounodus*. Among the other taxa recognised as Anisolambdinae (Cifelli 1983*a*) or Anisolambdidae (Soria 2001) and comparable with *Bounodus*, is *Anisolambda* Ameghino, 1901, which includes as synonyms a number of taxa represented only by isolated teeth (*Josepholeydia* Ameghino, 1901; *Ricardolydekkeria* Ameghino, 1901; *Heterolambda* Ameghino, 1904; *Lopholambda* Ameghino, 1904; *Eulambda* Ameghino, 1904; see Simpson 1948; Paula Couto 1952; Cifelli 1983*a*; Soria 2001). The molars in *Anisolambda* have a very weak or scarcely developed hypocone that tends to fuse at the base of the protocone, contrasting with the important development of the hypocone in *Bounodus*. Amongst Proterotheriidae the transition from bunoselenodonty to selenodonty is evident in forms such as *Proterotherium cervioides* Ameghino, 1883 from the late Miocene, whereas within the Megadolodontinae there are bunodont forms with very thick enamel, with a molar structure similar to that of Didolodontidae 'condylarthrans'. But, as Cifelli & Villarroel (1997) stated, beyond this dental pattern which is generally interpreted as primitive, *Megadolodus molariformis* shares with other Litopterna the high degree of molarisation of P4 that shows a subjugal and well separated paracone and metacone, well developed conules and strong cingulae. It mainly differs from true molars in the absence of a hypocone.

In addition, some advanced skeletal characters may be recognised, such as the presence of a spool-shaped astragalar body, lacking an upper astragalar foramen and possessing strong tibial and fibular crests, and an anteroposteriorly elongate and concave sustentacular facet of the calcaneum (Cifelli 1983*b*; Bergqvist 1996). Unfortunately, we still have no record of the postcranium of the new taxon. According to its dentition, it could fit with the supposed diet of the Laventan species of Colombia, *Megadolodus molariformis*, since the marked bunodonty and the thick enamel agree with an omnivorous diet including fruits with thick and strong rinds. In view of the environment that would have prevailed during the deposition of the Upper Member of the Urumaco Formation (Aguilera 2004), such a strong dentition would have been useful for breaking the exoskeletons of crustaceans or even molluscs. However, it is noteworthy that a bunodont dentition such as the one described, could not only have been an adaptive feature, but also a consequence of the persistence of a plesiomorphic character.

Acknowledgements

We wish to thank C. Villalba and A. Pulgar for help and camaraderie in the field; Dr O. Aguilera for his hospitality and assistance during the work of A. A. Carlini in Venezuela; Drs M. Reguero (MLP) for allowing us to access the collection of his institution; Dr M. Bond for critical review of the manuscript; Dr R.H. Madden for casts of *Megadolodus molariformis*; the two reviewers, Dr B. Shokey and Dr D Croft, for their valuable comments and suggestions which certainly improved our manuscript; and Dr C. Deschamps for the English translation of the manuscript. Illustrations are the work of A. Viñas. The work of A. A. Carlini in Venezuela was supported by the Committee for Research and Exploration of the National Geographic Society (Grant 7600-04 to M. R. Sánchez-Villagra) and PICT-R 0074 G3 (to A. A. C.). Finally, we wish to specially thank M. R. Sánchez for inviting us to study this wonderful fauna in Venezuela.

References

Aguilera, O. 2004. *Tesoros paleontológicos de Venezuela: Urumaco, patrimonio natural de la Humanidad*. Universidad Nacional Experimental F. de Miranda. Ed. Arte: Coro, Venezuela, 148 pp.

Ameghino, F. 1883. Sobre una colección de mamíferos fósiles del piso mesopotámico de la formación patagónica recogidos por el Prof. Pedro Scalabrini. *Boletín de la Academia Nacional de Ciencias de Córdoba* **5**: 101–116.

— 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en terrenos eocenos de la Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata* **1**: 1–26.

— 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas Academia Nacional Ciencias Córdoba* **6**: i-xxxii, 1–1027; Atlas, 98 figs.

— 1897. Mamiferés crétacés de l`Argentine. (Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*). *Boletín del Instituto Geográfico de Argentina, Buenos Aires* **18**: 431–521.

— 1901. Notices préliminaires sur des ongulés noveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* **16**: 349–426.

— 1902. Notices préliminaires sur des mammifères noveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba* **17**: 5–70.

— 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina* **57**: 327–341; **58**: 35–41.

Berg, C. 1899. Substitución de nombres genéricos. *III Comunicaciones del Museo Nacional de Buenos Aires* **1**: 77–80.

Bergqvist, L. P. 1996. *Reassociação do pós-cranio as espécies de ungulados da bacia de S. J. de Itaboraí (Paleoceno), estado do Rio de Janeiro, e filogenia dos 'Condylarthra' e ungulados sul-americanos com base no pós-cranio*. Ph D thesis: Porto Alegre, Universidade Federal do Rio Grande do Sul, 407 pp.

Bonaparte, J. & Morales, J. 1997. Un primitivo Notonychopidae (Litopterna) del Paleoceno Inferior de Punta Peligro, Chubut Argentina. *Estudios Geológicos* **53**: 263–274.

Cifelli, R. L. 1983*a*. The origin and affinities of the South American Condylarthra and Early Tertiary Litopterna (Mammalia). *American Museum Novitates* **2772**: 1–49.

— 1983*b*. Eutherian tarsals from the late Paleocene of Brazil. *American Museum Novitates* **2761**: 1–31.

— **& Guerrero, J.** 1997. Litopterns. Pp. 289–302 *in* R. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn (eds) *Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press: Washington and London.

— **& Guerrero Diaz, J.** 1989. New remains of *Prothoatherium colombianus* (Litopterna, Mammalia) from the Miocene of Colombia. *Journal of Vertebrate Paleontology* **9**: 222–231.

— **& Villarroel, C.** 1997. Paleobiology and affinities of *Megadolodus*. Pp. 265–288 *in* R. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn (eds) *Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press: Washington and London.

Hoffstetter, R. & Soria, M. F. 1986. *Neodolodus colombianus* gen. et. sp. nov., un noveau Condylarthre (Mammalia) dans le Miocène de Colombia. *Comptes Rendus de l'Académie des Sciences*, Paris Série II **303** (17): 1619–1622.

Hopwood, T. 1928. *Gyrinodon quassus*, a new genus and species of toxodont from western Buchivacoa (Venezuela). *Quarterly Journal of the Zoological Society of London* **84**: 573–583.

Linares, O. 2004. Bioestratigrafía de la fauna de mamíferos de las Formaciones Socorro, Urumaco y Codore (Mioceno Medio-Plioceno Temprano) de la región de Urumaco, Falcón, Venezuela. *Paleobiología Neotropical* **1**: 1–26.

McKenna, M. C. 1956. Survival of primitive Notoungulates and Condylarths into the Miocene of Colombia. *American Journal of Science* **254**: 736–743.

— & Bell, S. K. 1997. *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 631 pp.

Ministerio de Energía y Minas. 1997. *Léxico estratigráfico de Venezuela (Tercera Edición). Ministerio de Energía y Minas, Boletín de Geología* **12**: 1–818.

Odreman Rivas, O. E. 1969. Los Polymorphinae, un diferente tipo adaptativo de los Proterotheriidae (Mammalia, Litopterna). *Ameghiniana* **4**: 57–65.

Pascual, R. 1954. Adiciones a la fauna de la Formación de los Llanos de San Luis y su edad. *Revista del Museo de Ciencias Naturales y Tradicional de Mar del Plata* **1**: 113–121.

Paula Couto, C. de. 1952. Fossil mammals from the beginning of the Cenozoic in Brasil. Condylarthra, Litopterna, Xenungulata and Astrapotheria. *Bulletin of the American Museum of Natural History* **99**: 355–394.

Roth, S. 1899. Aviso preliminar sobre mamíferos patagónicos encontrados en Patagonia. *Revista del Museo de La Plata* **9**: 381–388.

Simpson, G. G. 1948. The begining of the age of mammals in South America. Part 1. Introduction. Systematics: Marsupialia, Edentata, Condylarthra, Litopterna, Notioprogonia. *Bulletin of the American Museum of Natural History* **91**: 1–232.

Soria, M. F. 2001. Los Proterotheriidae (Litopterna, Mammalia), sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales* **1**: 1–167.

— & Hoffstetter, R. 1983. Présence d'un Condylarthre (*Salladolodus deuterotheroides* gen. et. sp. nov.) dans le Déséadien (Oligocène inférieur) de Salla, Bolivie. *Comptes Rendus de l'Académie des Sciences Paris* **297**: 267–270.