

A NEW SPECIMEN OF TOXODONTIDAE (NOTOUNGULATA) FROM THE URUMACO FORMATION (UPPER MIOCENE) OF VENEZUELA

Mariano Bond

Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

Richard H. Madden

Department of Biological Anthropology & Anatomy, Box 3170 Duke University Medical Center, Durham, North Carolina 27710, USA

Alfredo A. Carlini

Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina and CONICET, Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina

SYNOPSIS A new specimen of Toxodontidae, consisting of a partial mandibular ramus with three molars, is described from the Middle Member of the Urumaco Formation and compared with type and referred material from all four taxa previously reported from Venezuela and with several better known taxa of advanced Toxodontidae. Incomplete preservation and postmortem distortion make an assessment of its morphology difficult. Despite these shortcomings, the new material does not appear to represent any of the Venezuelan taxa previously described. The specimen shows a unique combination of characters including a pattern of lingual enamel folds, weakly developed meta-entoconid and well-developed ento-hypoconid fold (m₁ and m₂, not in m₃), subrounded and lingually expanded trigonid, transversely broad hypoconid and open labial enamel fold. In this combination of features, the new specimen most closely resembles the types of *Trigodonops lopesi* and *Mixotoxodon larensis*.

KEY WORDS Urumaco Formation, fossil mammal, Neogene, South America

Contents

Introduction	285
Abbreviations	287
Systematic palaeontology	287
Notoungulata Roth, 1903	287
Toxodontia Owen, 1853	287
Toxodontidae Gervais, 1847	287
Toxodontidae indet.	287
Discussion	289
Acknowledgements	291
References	291

INTRODUCTION

The Toxodontidae (Toxodontia, Notoungulata) is a clade of endemic South American ungulates of medium to very large size that are common and geographically and temporally widespread through the Oligocene to late Pleistocene (Deseadan through Lujanian). Toxodontidae are also known in North America from Pleistocene age deposits in Honduras

and El Salvador. Toxodontidae were among the first notoungulates to be described in the scientific literature. *Toxodon platensis* Owen, 1837, was based on a specimen collected by Darwin in 1833 (Bond 1999). Toxodontidae is one of the more diverse groups of notoungulates. Taxa included in the family share a relatively derived arrangement of anterior teeth involving a transversely broad array of heteromorphic incisors and incisor tusks. They evolved high-crowned or

hypsodont teeth early in their evolutionary history and ever-growing cheek-teeth by the Middle Miocene. In addition, the evolutionary history of the family involved progressive simplification of the tooth crown pattern after the Middle Miocene. Many taxa of Toxodontidae have been described on the basis of fragmentary material, mostly dental remains, without sufficient samples to permit a full appreciation of the ontogenetic and intraspecific variation. It is likely that many of the described taxa listed by Mones (1986) will prove to be invalid with the discovery of more complete material and more numerous samples.

Kraglievich (1934) made a series of observations about Toxodontidae and its possible suprageneric groups. Subsequently, Pascual (1965) undertook the first modern systematic revision of the more recent members of the family (Middle Miocene–Pleistocene taxa), recognising the relatively primitive Nesodontinae (Oligocene to early Miocene), the morphologically specialised Xotodontinae and two subfamilies of more derived taxa, the Toxodontinae and the Haplodontheriinae. Later, Madden (1997) proposed a new subfamily of advanced Toxodontidae, the Dinotoxodontinae (including *Pericotoxodon* Madden, 1997, *Gyrinodon* Hopwood, 1928 and *Dinotoxodon* Mercerat, 1895), on the basis of dental characters and presumably unique mandibular morphology. However, with the discovery and description of *Hoffstetterius imperator* Saint-Andre, 1993, from Bolivia, Saint-Andre (1993) could not confirm the validity of the ‘Dinotoxodontinae’.

Most recently, Nasif *et al.* (2000) undertook an explicit phylogenetic analysis of the family and recognised only two subfamilies, the Nesodontinae and the Toxodontinae. They included in this latter group all those taxa that had been formerly included in Xotodontinae, Haplodontheriinae or Dinotoxodontinae. Nasif *et al.* (2000) did not consider all of the numerous described taxa in their analysis, in particular omitting those based on fragmentary remains or that were incompletely known.

To date, four taxa of Toxodontidae have been described or mentioned for northern Venezuela, *Gyrinodon quassus* Hopwood, 1928, *Mixotoxodon larensis* Van Frank, 1957, *Alitoxodon* sp. and *Ocnerotherium* sp. The holotype of *Gyrinodon quassus*, BMNH 13158 (formerly BMGD, see below), is a left mandibular ramus with the crowns of m1–m3 broken at the alveolar margin. Together with the mandibular ramus and, presumably, from the same individual, are isolated upper teeth including right I2, P2, P3, M1? and M3 and left P4 and M2?, skull cap and miscellaneous postcranial elements. The upper teeth of *Gyrinodon quassus* have never been adequately described or figured. All of this material was collected in the ‘La Puerta Formation’ in western Buchivacoa, Falcón, Venezuela. The existence of material of *Gyrinodon* from the Urumaco Formation has been recorded by Linares (2004).

Paula Couto (1982) referred isolated lower molars from Acre Province (Brazil) to *Gyrinodon*. This referred material includes AMNH 55788, right m1 or m2 (Paula Couto 1982: fig 9A), AMNH 55779 and 55781, talonids of m1 or m2 (Paula Couto 1982: figs 10A and 10B) and DGM 532-M (left m2?) (Paula Couto 1982: fig 11A), DGM 545-M talonid of left m1 or m2 (Paula Couto 1982: fig 12), DGM 531-M fragmentary talonid of left m3 (Paula Couto 1982: fig. 13) and AMNH 55733 fragments of left m3 (Paula Couto 1982: fig. 14). Additional material from Acre has recently been

assigned to this genus, including upper and lower teeth (Bocquentin & Silva 1994: fig. 2).

Mixotoxodon larensis Van Frank, 1957 was described on the basis of holotype AMNH 48854, the symphyseal portion of a mandible preserving left i1 and i2, right i1 to p3 and most of p4; and a number of paratypes including AMNH 48851, a partial left ramus with m1–3 and AMNH 48852, a partial right ramus with p4, m1–3. In addition, isolated upper teeth were referred to the same species (Van Frank 1957: figs 9–10). The type material of *Mixotoxodon larensis* was collected near the town of San Miguel south-west of Barquisimeto, Lara State. Material referred by Van Frank (1957) to *Mixotoxodon larensis* includes specimens from Honduras (McGrew 1942) and El Salvador (Stirton & Gealey 1949; Webb & Perrigo 1984). Finally, Porta (1959) referred a partial right mandibular ramus with p4–m2 from northern Colombia to the same species.

Linares (2004) recently mentioned the presence of a third taxon from a higher stratigraphic level in the Urumaco Formation, *Ocnerotherium* Pascual (1954). *Ocnerotherium intermedium* Pascual, 1954 (the only known species of the genus) was established on the basis of a fragmentary right maxilla with P1–M3 and an associated mandibular fragment with p4 and another with right m2 and the trigonid of m3 (MLP 52-IX-17-1), from San Luis Province, Argentina. In the same paper, Linares (2004) also mentioned the presence of *Alitoxodon* sp., based on a lower jaw of a young adult. The type species of *Alitoxodon*, *A. vetustus* Rovereto, 1914, is from the Montehermosan (Pliocene) of Argentina and is based on a lower jaw with deciduous molars (MACN 7835); the other species referred to this genus *A. excavavatus* (Rovereto, 1914; see Kraglievich 1934) is based on a lower jaw with poorly preserved dentition (MACN 2931), not fully described and, very curiously, figured from its ventral side (Rovereto 1914: pl. 10, fig. 6).

In addition to the material listed above, we have also examined isolated and fragmentary teeth of Toxodontidae indet. from the Urumaco Formation in the collection of the UNEFM in Coro.

Other taxa of Tertiary Toxodontidae have been described from Colombia and elsewhere in tropical South America. These include *Pericotoxodon platignathus* Madden, 1997 from Colombia and *Trigodonops lopesi* Kraglievich, 1930 (Roxo 1921) from Brazil (see Paula Couto 1956). Less well-known taxa, including *Abothrodon pricei* Paula Couto, 1944 and the numerous taxa proposed by Paula Couto (1982), are mostly based on rather sparse material from Acre in Brazil.

There is, as yet, nothing from Bolivia that is morphologically comparable to this new specimen from Venezuela. However, we have made limited comparisons with *Hoffstetterius imperator* because of the importance of this taxon to our understanding of character distribution amongst advanced Toxodontidae. Finally, we extend our comparisons somewhat more broadly to two somewhat better known taxa from the late Miocene of Argentina and Uruguay, *Dinotoxodon paranensis* and *Pisanodon (Palaeotoxodon) nazari*.

We have restricted our comparisons to the better-known taxa of advanced Toxodontinae from tropical and subtropical latitudes in South America, not because of any geographical bias in our experience, but because of the broad morphological similarity we find with the new material described here. Whether this morphological similarity reflects underlying

Table 1 Measurements (in mm) of the lower molars of Venezuelan Toxodontidae

	UNEFM-CIAAP 616	<i>Gyrinodon quassus</i> [†] M13158	<i>Mixotoxodon larensis</i> [‡] AMNH 48852
m1 length	48	39.5	48
m1 trigonid breadth	–		19
m1 trigonid length			13.5
m2 length	45.8	40.5	46
m2 breadth	–		21
m2 trigonid length	12.9		14
			AMNH 48851
m3 length	65.7	62	71?
m3 trigonid breadth	18.2		19
m3 trigonid length	11.2		13

[†]From Hopwood (1928: 573).

[‡]From Van Frank (1957: table 4).

phylogenetic affinity is a question that requires more comprehensive analysis, which we do not attempt given our concerns about the adequacy of the new material.

To check ontogenetic variation we examined juvenile and adult material of *Pericotoxodon*, *Dinotoxodon* and *Pisanodon* that were at our disposal. In addition all of the referred material of *Gyrinodon*, *Dinotoxodon* and *Mixotoxodon* together provide some additional constraints on the scope of individual variation within single species of derived Toxodontidae that have simplified lower molar morphology.

Abbreviations

ACH, Achiri, Bolivia; **AMNH**, American Museum of (Natural History), New York, New York; **BMGD**, British Museum Geology Department; **BMNH**, British Museum (Natural History), London; **DGM**, Departamento de Geología e Mineralogía; **DPV-FC**, Departamento de Paleontología de Vertebrados, Facultad de Ciencias, Montevideo, Uruguay; **ICN**, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; **MLP**, Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **OC**, Quebrada de Ocando, Urumaco, Falcón, Venezuela; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **UFAC**, Universidade Federal do Acre, Rio Branco, Brasil; **UNEFM-CIAPP**, Universidad Nacional Experimental Francisco de Miranda, Coro, Falcón, Venezuela.

SYSTEMATIC PALAEOLOGY

NOTOUNGULATA Roth, 1903

TOXODONTIA Owen, 1853

TOXODONTIDAE Gervais, 1847

Toxodontidae indet. (Fig. 1)

REFERRED MATERIAL. UNEFM-CIAAP 616, a portion of left mandibular ramus with the base of the ascending ramus and m1 to m3.

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

DESCRIPTION. The specimen offers only characters of the horizontal ramus and the crown patterns of m1 to m3 for comparison and has evidently been eroded on its lingual side (Fig. 1B). The quality of preservation diminishes from m1 to m3, making details of crown structure more difficult to ascertain on m2 and m3, especially crown proportions, the distribution of enamel on the lingual aspect and the depth and constancy of the lingual enamel folds. Establishing what part of the observed morphology is real and what part was subject to postmortem distortion, is necessary before we can determine which features, if any, are unique and which are shared with other taxa of Toxodontidae.

The specimen comes from an older adult, given the relative length of m3 (Table 1). The mandibular ramus is so poorly preserved that it is not possible to establish the depth of the ramus nor determine definitively whether the inferior margin was expanded inferolaterally as in *Gyrinodon quassus*, *Dinotoxodon paranensis*, *Pericotoxodon platignathus*, *Mixotoxodon larensis* and some other Toxodontidae. The inferior margin of the ramus is inferolaterally expanded in *Mixotoxodon larensis* and the specimen referred to this species by Porta (1959). A published photograph of UNEFM-CIAAP 616 taken before final cleaning and preparation (Aguilera 2004), suggests a deep mandibular corpus, as deep as that seen in older individuals of *Pericotoxodon platignathus*. In incompletely preserved specimens of *Dinotoxodon* and *Pericotoxodon*, where the inferior margin of the mandible is broken away and the margin is not preserved, it is still possible to infer that the ramus was expanded inferolaterally by the outline contours of the ramus in transverse cross-section. In taxa with mandibles that develop an inferolaterally expanded ramus (e.g. *Pericotoxon platignathus*), the cross-sectional outline of the ramus at m1/m2 (but especially at the level of m3) is concave labially and convex lingually (see Madden 1997: fig. 21.3). These contours are not bilaterally symmetrical, but rather the anteroposterior axis of the labial concavity occurs at a higher level on the ramus whereas the anteroposterior axis of the lingual convexity is set at a level beneath the pulp cavities of the molars. This configuration is unmistakable and very different from that observed in taxa

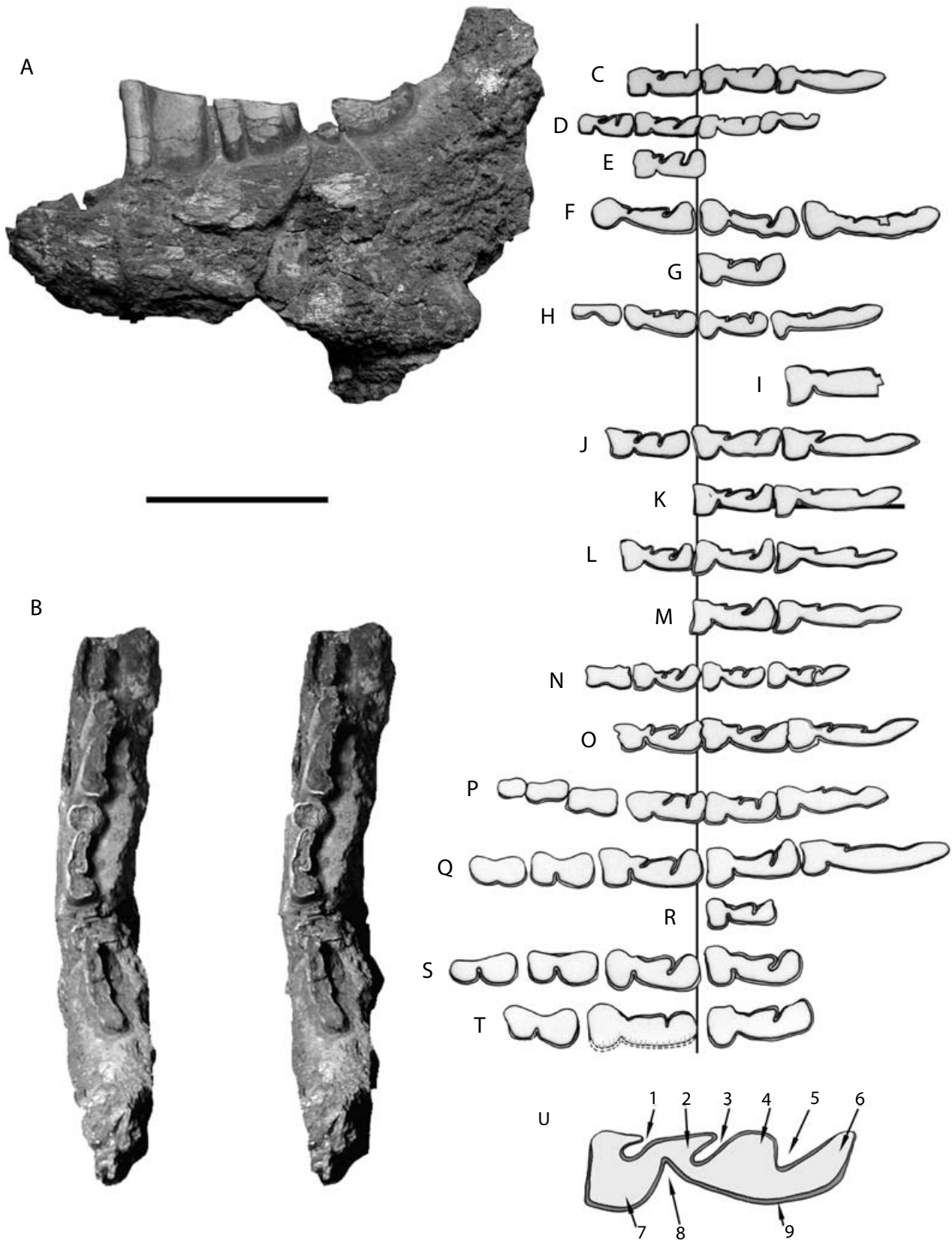


Figure 1 (A), (B) Toxodontidae indet. UNEFM-CIAAP 616, partial left mandible with m1–3, from Urumaco Formation (Upper Miocene), Urumaco, Venezuela. **A**, labial view; **B**, stereopair in occlusal view. **C–T**, occlusal views of the mandibular molar series in various Late Miocene Toxodontidae. **C**, '*Pisanodon*' (= *Palaeotoxodon*) *nazari*; MLP 76-VI-12-132, left m1–m3; Las Barrancas Member, Arroyo Chasico Formation, Partido Villarrino, Buenos Aires Province, Argentina. **D**, '*Pisanodon*' (= *Palaeotoxodon*) *nazari*; MLP 60-VI-18-63, juvenile left dp4, m1–m3

that do not display the deepened and inferolaterally expanded ramus. The concavity of the labial aspect can be observed in even rather poorly preserved material.

The three lower molars are hypsodont and very probably ever-growing. The crowns are elongate anteroposteriorly and narrow transversely, as is typical of advanced Toxodontidae (e.g. *Toxodon platensis*). The crowns are broadest at the trigonid, which extends lingually in subrounded and enameless contour (as in *Trigodonops lopesi*, but different to *Gyrinodon quassus*: see Figs 1F, 1J 1S). The hypoconid lobe is broad transversely on m1 and especially on m2 (as in *Trigodonops lopesi*). On the lingual side, the weakly developed meta-entoconid fold makes the molar appear shorter anteroposteriorly than in other Toxodontidae (e.g. *Gyrinodon quassus*). On the lingual side of the crown the trigonid terminates posteriorly at the point of an inflection in the lingual enamel band. Assuming this inflection to be a remnant of the meta-entoconid fold, its position on m1 and m2 indicates that the meta-entoconid fold was positioned somewhat more anteriorly than usual in Toxodontidae (Fig. 1).

As in all other advanced Toxodontidae (Pascual 1965; Nassif *et al.* 2000), enamel is not continuous around the circumference of the crown, but is interrupted on the lingual side anteriorly and posteriorly. The labial enamel fold separating the trigonid and talonid is well marked but shallow and open, especially on m1 and m3. The ento-hypoconid fold is relatively better developed than the meta-entoconid fold, especially on m2. The ento-hypoconid fold was probably also present on m3, but is poorly preserved and its configuration difficult to reconstruct. The middle lobe of the talonid or entoconid is flat lingually rather than rounded or convex.

In occlusal view the labial enamel of m2 and m3 is irregularly undulated and this is unusual among Toxodontidae because the labial enamel of lower molars generally displays regular or smooth curvatures. Only the slight inflection of the labial enamel near the posterior end of m3 appears to reflect real morphology. The third molar in *Dinotoxodon* (MLP 41-XII-13-4, MLP 57-X-10-123, MLP 39-XII-2-8) presents a characteristic narrowing of the talonid of the crown at the level of the ento-hypoconid fold, such that the posterior-most lobe or hypoconid in m3 is narrower transversely than the middle lobe or entoconid. However, with the exception of this feature, irregular undulations in the labial enamel, such as are seen on m2 and m3 in UNEFM-CIAAP 616, are

unusual and no other Toxodontidae displays similar irregular undulations.

In addition to the irregularities of the labial enamel on m2 and m3, the lower molar crowns (especially m2 and m3) are narrow and their proportions seem to be unique among Toxodontidae (Table 1). This suggests that the m2 and m3 crowns are compressed laterally. In addition, the long axes of these crowns are concave in occlusal view and the m2 hypoconid is displaced out of its usual alignment such that the posterior face of the hypoconid is not perpendicular to the long axis of the crown, but instead is inclined anterolingually. The posterior end of the talonid in m3 is similarly out of alignment with the long axis of the crown. The torsion or curvature of the long axes of m2 and m3 is probably additional evidence of postmortem distortion. These displacements explain the irregular undulations of the labial enamel, the poor preservation of the lingual enamel and lingual enamel folds on m3 and the many expanded fractures on the labial side of m2 and m3 crowns. Of the three molar crowns, the first molar is least affected by postmortem distortion and reveals no irregular undulations of the labial enamel and is the broadest of the three molars. Thus, we hesitate to give significance to the crown proportions of m2 and m3 and some of the peculiarities of the arrangement of their lingual enamel folds.

In measurement, the m1 crown is longer than the m2 crown (Table 1). Generally, in Toxodontidae, m1 and m2 are nearly equal in length, with m1 slightly subequal. Toxodontidae with m1 longer than m2 are unusual and among the taxa included here for comparison, this is observed only in *Mixotoxodon larensis* (AMNH 48852) (Fig. 1Q, Table 1).

DISCUSSION

The pattern of lingual enamel folds in UNEFM-CIAAP 616, wherein a weakly developed meta-entoconid fold occurs in combination with a better developed ento-hypoconid fold, is not unique among Toxodontidae. This pattern is found to some degree in material of *Pisanodon* (MLP 76-VI-12-132), *Dinotoxodon* (MLP 41-XII-13-4, MLP 57-X-10-123, MLP 39-XII-2-8), *Mixotoxodon* (AMNH 48851-48852) and *Trigodonops* (DGM 55-M).

While it is usually the case among Toxodontidae that m1 and m2 have similar patterns of lingual folds, in some taxa m1 folds are better developed and more persistent than those of

(erupting); lower level (Vivero Member?), Arroyo Chasico Formation, Buenos Aires Province, Argentina. **E**, '*Pisanodon*' (= *Palaeotoxodon nazari*); MLP 60-VI-18-63, m1 crown outline at base. **F**, CIAAP 616 reconstructed left m1 to m3 from the middle Urumaco Formation, Venezuela. **G**, cf. *Gyrinodon* sp.; UFAC 1417 m1 or 2, from Bocquentin & Silva (1994: fig. 2g) **H**, cf. *Gyrinodon* sp.; UFAC 1292 m1–m3 and UFAC 1413 p4 from Bocquentin & Silva (1994: figs 2f, h). **I**, ?*Gyrinodon quassus*; OC-69 (636), partial left m3. **J**, *Gyrinodon quassus*; BMNH M13158 (holotype) mandibular m1–3. **K**, *Dinotoxodon paranensis*; MLP 41-XII-13-4, right m2–3 (reversed), Ituzaingo Formation, east bank, Paraná River, Entre Rios Province, Argentina. **L**, *Dinotoxodon paranensis*; MLP 57-X-10-123, left m1–3, Ituzaingo Formation, East Bank Paraná River, Entre Rios Province, Argentina. **M**, *Dinotoxodon paranensis*; MLP 39-XII-2-8, left m2–3, El Brete, Paraná, Entre Rios Province, Argentina; Formación Ituzaingo. **N**, *Dinotoxodontinae* indet.; FC-DPV-902, juvenile left dp4, m1–m3, Barrancas de San Gregorio, Departamento San José, Uruguay. **O**, cf. *Dinotoxodon*; FC-DPV-514, adult right m1–3 (reversed), Playa Sánchez, Departamento San José, Uruguay; Camacho Formation (Lithofacies Kiyú). **P**, *Hoffstetterius imperator*; MNHN ACH 1 (holotype), right p2–m3 (reversed), Achiri, Bolivia. **Q**, *Mixotoxodon larensis*; AMNH 48854 right p2–4, AMNH 48852 right m1–2, AMNH 48851 right m3. **R**, *Mixotoxodon larensis*; UCMP V4201/37040, El Salvador. **S**, *Trigodonops lopesi*; DGM 55-M (holotype), left p3–4, m1–2; Upper Juruá River, Acre, Brazil. **T**, *Mixotoxodon larensis crusafonti*; ICN 0135 (holotype), p4–m2. **U**, dental morphology and terminology in the lower molars of toxodontids (1, protoconid; 2, bucal enamel fold; 3, bucal enamel; 4, anterior fold; 5, metaconid; 6, meta-entoconid fold; 7, entoconid, entolophid; 8, ento-hypoconulid fold; 9, hypoconulid). Scale bar = 10 cm.

m2. This is the case in *Mixotoxodon*, *Hoffstetterius* (MNHN ACH 1), *Dinotoxodon*, *Pisanodon* and also *Gyrinodon quassus* Hopwood, 1928. By contrast, in UNEFM-CIAAP 616 the ento-hypoconid fold is better developed on m2 than on m1, but we are unsure whether postmortem distortion has influenced this peculiarity. An open ento-hypoconid fold such as that of the m2 in UNEFM-CIAAP 616 is also found in material of *Dinotoxodon* from northeast Argentina, although not in the material referred to *Dinotoxodon* from Uruguay (DPV-FC 902). The peculiar combination of weakly developed meta-entoconid fold and well-developed and open ento-hypoconid fold is only found in material of *Dinotoxodon* from the Ituzaingó Formation in Entre Rios Province, Argentina.

The combination of weakly developed meta-entoconid fold, well-developed ento-hypoconid fold and transversely broad m1 and m2 hypoconid is observed in *Mixotoxodon*, *Dinotoxodon* and *Trigodonops*. However, the combination of these three features plus an open labial fold is not known in any other Toxodontidae and this combination of features makes UNEFM-CIAAP 616 particularly interesting and noteworthy. We hesitate to ascribe taxonomic significance to this unique combination of characters because of our lack of knowledge about age-related variation in the labial and lingual folds and the uncertain extent of postmortem distortion.

Individual variation and patterns of age-related variation in the lingual enamel folds in advanced Toxodontidae are difficult to sort out given our present understanding. No good samples of material representing the full age-range within a single species are yet available for any advanced Toxodontidae except *Pericotoxodon platignathus* and this sample indicates relatively little variation in the lower molar lingual folds. However, juvenile and adult specimens of *Pisanodon* (MLP 76-VI-12-132, MLP 60-VI-18-63) suggest instability in the arrangement of m1 lingual folds. In this taxon, the m1 lingual folds actually become better developed and more deeply penetrant in older individuals. The same is true for the Uruguayan material referred to *Dinotoxodon* (DPV-FC 902, DPV-FC 514) (Figs 1K-1O). Our observations suggest that the arrangement of lingual folds in UNEFM-CIAAP 616 should provide a basis for resolving its taxonomic affinity.

With regard to lower molar crown proportions, there is relatively little variation within the single species sample of *Pericotoxodon platignathus* (Madden 1997). By contrast, however, there is considerable variation in m3 crown proportions among adults of *Dinotoxodon paranensis*. Thus, in addition to our concerns about the extent of the influence of postmortem distortion on crown proportions in UNEFM-CIAAP 616, individual variation in m3 crown proportions can be considerable.

UNEFM-CIAAP 616 was tentatively identified as a specimen of *Gyrinodon* by Aguilera (2004). *Gyrinodon*, a toxodontid whose only known species is *G. quassus* Hopwood 1928, was collected from beds of unknown age in western Falcón State, Venezuela (Hopwood 1928; see also Van Frank 1957). Among the original material of *G. quassus* are upper teeth whose morphology was never adequately described and yet is critical for the taxonomic assessment of material subsequently referred to *Gyrinodon* by other workers, including the material from Acre (Paula Couto 1982) and UFAC 1292 and 1417 (Bocquentin & Silva 1994). We note that Nasif *et al.* (2000) mentioned the presence of *Gyrinodon* in Bolivia

in addition to its occurrences in Venezuela and Brazil, without providing information about the source of the evidence for this claim.

A more detailed and critical examination of UNEFM-CIAAP 616 from the Urumaco Formation, reveals a series of characters of lower molar crown morphology that makes its referral to *Gyrinodon quassus* problematical. Among the differences, we note the following: (1) the trigonid is shorter antero-posteriorly on the lingual side and does not display a postero-lingually projecting metaconid, (2) the meta-entoconid fold is less well developed, (3) the m1 ento-hypoconid fold is less pronounced and more shallow, (4) the labial fold is open and does not penetrate as far into the substance of the crown and (5) the entoconid is narrow in transverse breadth and flattened lingually. These contrasts make referral of UNEFM-CIAAP 616 to *Gyrinodon* untenable.

Expanding the hypodigm still further by including UFAC 1292 stretches the concept of this species beyond what we find acceptable given the proportions of the m2 and m3 trigonids as depicted by Bocquentin & Silva (1994: fig. 2h).

Referral of UNEFM-CIAAP 616 to *Mixotoxodon larensis* is indefensible, with the following differences between UNEFM-CIAAP 616 and the type material of *Mixotoxodon larensis*: (1) the lower molar crowns of UNEFM-CIAAP 616 are narrower; (2) UNEFM-CIAAP 616 displays more rounded trigonids anteriorly with enamel extending farther lingually on the anterior face; (3) the m3 talonid in UNEFM-CIAAP 616 does not taper gradually posteriorly as it does in *Mixotoxodon larensis*; (4) the m1 lingual folds are less well-developed and less penetrant; and (5) the lower molar labial folds are open, not closed or appressed as in *Mixotoxodon larensis*. Of these differences, the narrow crown proportions may be a consequence of postmortem distortion (see above). The development of the m2 metaconid and open labial folds may reflect individual or age differences between UNEFM-CIAAP 616 and the type of *Mixotoxodon larensis* Van Frank, 1957.

Comparison of UNEFM-CIAAP 616 to *Ocnerotherium intermedium* Pascual, 1954 is made difficult by the incompletely preserved lower molar material of the type of that taxon (see Pascual 1954). *Ocnerotherium intermedium* is comparable in size to *Mixotoxodon larensis* and UNEFM-CIAAP 616. However, compared with UNEFM-CIAAP 616, the m2 and preserved parts of m3 are much broader in their proportions while m2 has a broad entoconid and distinct meta-entoconid and ento-hypoconid folds lingually in *O. intermedium*. Furthermore, the anterior face of the trigonid and posterior face of the talonid on the m2 of *O. intermedium* are perpendicular to the long axis of the crown. In these characters, *O. intermedium* is very different from UNEFM-CIAAP 616 and we cannot therefore refer UNEFM-CIAAP 616 to this taxon.

The type species of *Alitoxodon*, *A. vetustus*, differs from UNEFM-CIAAP 616 in that the m1 and m2 have distinct lingual meta-entoconid and ento-hypoconid folds lingually and the labial fold separating the trigonid and talonid is more distinct. Furthermore, the trigonids of m1 and especially of m2 are not lingually expanded as in UNEFM-CIAAP 616; in *A. excavatus*, the poorly preserved m1–m3 apparently show distinct meta-entoconid and ento-hypoconid lingual folds. These differences prevent us from referring UNEFM-CIAAP 616 to *Alitoxodon*.

In conclusion, UNEFM-CIAAP 616 cannot be referred to *Gyrinodon quassus*, *Mixotoxodon larensis*, *Ocnerotherium intermedium*, *Alitoxodon vetustus* or *A. excavatus*. We prefer to maintain this new specimen as *Toxodontinae incertae sedis* until more complete and undistorted material becomes available.

ACKNOWLEDGEMENTS

We wish to thank M. E. Gómez, M. López and A. Pulgar at the CIAAP, for their assistance and permission to study the collections under their care; 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) and A. Kramarz (MACN) for allowing us access to the collection of their respective institutions; the two reviewers, Dr M. Reguero and an anonymous reviewer, for their valuable comments and suggestions which certainly improved our manuscript. Illustrations are the work of J. Gonzalez. 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 specially to thank M. R. Sánchez-Villagra for inviting us to study this wonderful fauna in Venezuela.

REFERENCES

- Aguilera, O. A. 2004. *Tesoros Paleontológicos de Venezuela: Urumaco, Patrimonio Natural de la Humanidad*. Editorial Arte: Coro, Venezuela, 148 pp.
- Bocquentin, J.-C. & Silva, W. 1994. Cf. *Gyrinodon* sp. (Notoungulata, Toxodontidae) proveniente do mioceno superior da localidade Cavalcante, Acre, Brasil. *Acta Geologica Leopoldensia, Edição Especial (Congresso Brasileiro de Paleontologia, 1994, São Leopoldo-RS), Universidade do Vale do Rio dos Sinos* 1: 391–398.
- Bond, M. 1999. Quaternary native ungulates of southern South America: a synthesis. Pp. 177–205 in J. Rabassa & M. Salemme (eds) *Quaternary of South America and Antarctic Peninsula*. A.A. Balkema: Rotterdam.
- Gervais, H. 1847. Observations sur les mammifères fossiles du midi de la France. *Annales des Sciences Naturelles, Zoologie* (3) 8: 203–224.
- Hopwood, T. 1928. *Gyrinodon quassus*, a new genus and species of toxodont from western Buchivacoa (Venezuela). *Quarterly Journal of the Geological Society, London* 84: 573–583.
- Kraglievich, L. 1930. Revindicação do genero *Carolibergia* Mercerat por Alipio de Miranda Ribeiro; critica bibliografica. *Physis* 10(35): 227–228.
- 1934. La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que la precedieron y sucedieron. *El Siglo Ilustrado, Montevideo* 938: 1–136.
- Linares, O. J. 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.
- Madden, R. H. 1997. A new genus of Toxodontidae from the Miocene Honda Group of Colombia. Pp. 333–352 in R. F. 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 DC.
- McGrew, P. O. 1942. Field Museum Paleontological Expedition to Honduras. *Science* (24 July 1942): 85.
- Mercerat, A. 1895. Molaires de Toxodon et d'autres représentants de la même famille. *Anales del Museo Nacional de Buenos Aires* 4: 207–215.
- Ministerio de Energía y Minas. 1997. *Léxico estratigráfico de Venezuela (Tercera Edición)*. Ministerio de Energía y Minas, Boletín de Geología 12, 818 pp.
- Mones, A. 1986. Palaeovertebrata Sudamericana: catálogo sistemático de los vertebrados fósiles de America del Sur. I. Lista preliminar y bibliografía. *Courier Forschungsinstitut Senckenberg* 82: 1–625.
- Nasif, N. L., Musalem, S. & Cerdeño, E. 2000. A new toxodont from the late Miocene of Catamarca, Argentina, and a phylogenetic analysis of the Toxodontidae. *Journal of Vertebrate Paleontology* 20: 591–600.
- Owen, R. 1837. A description of the cranium of the *Toxodon platensis* a gigantic extinct mammiferous species referable by its dentition to the Rodentia, but with affinities to the Pachydermata and the herbivorous Cetacea. *Proceedings of Geological Society of London* 2: 541–542.
- 1853. Description of some species of the extinct genus *Nesodon*, with remarks on the primary group (Toxodontia) of the hoofed quadrupeds to which that genus is referable. *Philosophical Transactions of the Royal Society of London* 143: 291–309.
- Pascual, R. 1954. Adiciones a la fauna de la Formación de Los Llanos de San Luís y su edad. *Revista del Museo Municipal de Ciencias Naturales y Tradicionales, Mar del Plata* 1: 113–121.
- 1965. Los Toxodontidae (Toxodonta, Notoungulata) de la Formación Arroyo Chásico (Plioceno Inferior) de la Provincia de Buenos Aires. *Ameghiniana* 4: 101–132.
- Paula Couto, C. 1944. Noticia preliminar sobre um novo Toxodonte do Cenozoico do Territorio do Acre, *Abothrodon pricei*. *Boletim Museum Nacional, Rio de Janeiro, n. ser., Geologia* 3: 1–4.
- 1956. *Mamíferos fósseis do Cenozóico da Amazonia*. Conselho Nacional de Pesquisas, Boletim 3. Instituto Brasileiro de Bibliografia e Documentação: Rio de Janeiro.
- 1982. Fossil mammals from the Cenozoic of Acre, Brazil, V. Notoungulata Nesodontinae (II), Toxodontinae and Haplodontheriinae, and Litopterna, Pyrotheria and Astrapotheria (II). *Iheringia, Serie Geologica* 7: 5–43.
- Porta, J. de. 1959. Nueva subespecie de toxodóntido del cuaternario de Colombia. *Boletim de Geologia, Universidad Industrial de Santander, Bucaramanga* 3: 55–61.
- Rovereto, C. 1914. Los estratos araucanos y sus fósiles. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 25: 1–247.
- Roth, S. 1903. Los ungulados sudamericanos. *Anales del Museo de La Plata. Sección Paleontología* 5: 1–36.
- Roxo, M. G. de O. 1921. *Note on a new species of Toxodon Owen, T. lopesi Roxo*. Empresa Brazil Editora: Rio de Janeiro.
- Saint-Andre, P.-A. 1993. *Hoffstetterius imperator* n. g., n. sp. du Miocene supérieur de l'Altiplano bolivien et le statut des Dinotoxodontinés (Mammalia, Notoungulata). *Compte Rendus de l'Académie des Sciences, Paris*, 316 (Série II): 539–545.
- Stirton, R. A. & Gealey, W. K. 1949. Reconnaissance geology and vertebrate paleontology of El Salvador, Central America. *Bulletin of the Geological Society of America* 60: 1731–1754.
- Van Frank, R. 1957. A fossil collection from northern Venezuela. I. Toxodontidae (Mammalia, Notoungulata). *American Museum Novitates* 1850: 1–38.
- Webb, S. D. & Perrigo, S. C. 1984. Late Cenozoic vertebrates from Honduras and El Salvador. *Journal of Vertebrate Paleontology* 4: 237–254.