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NEW REMAINS OF *Mixotoxodon larensis* Van Frank 1957 (Mammalia: Notoungulata) FROM MENE DE INCIARTE TAR PIT, NORTH-WESTERN VENEZUELA

ASCANIO D. RINCÓN

SUMMARY

Mixotoxodon larensis was a rhino-like mammal, which represents the northernmost Pleistocene toxodontid, and its remains are known from many localities in Central and South America. Biogeographically, *M. larensis* is an intertropical taxon because

its record spreads between 15°S (Bolivia) and 18°N (México). Here a new record is reported for this species at Mene de Inciarte tar pits, Sierra de Perija, Zulia State, Venezuela, with an age estimate of 25-27000 years old (Late Pleistocene).

Toxodontidae are medium to large terrestrial herbivorous Notoungulata, easily recognized by their specialized anterior dentition, ever-growing incisor tusks, and distinctive high-crowned molars (Madden, 1997). This family was widespread in South America during the Cenozoic, becoming very abundant in the Miocene. The first remains of these animals were found by Charles Darwin and described by Richard Owen (1837). The oldest record of the Toxodontidae Family comes from the Oligocene of Patagonia, southern Argentina. Toxodontids are also known from the Neogene of Brazil, Perú, Ecuador, Bolivia, Uruguay, Venezuela, and Colombia. During the Pleistocene they reached North America (Nasif et al., 2000).

From the Venezuelan Pleistocene, the first record of toxodontids is from El Tocuyo, Lara State, where *Toxodon* was recovered (Karsten, 1886). In 1928 *Gyrinodon quassus* was registered from the northwest of Buchivacoa (Hopwood, 1928) and has been attributed to the Huayquerian (Late Miocene) from Venezuela, Bolivia and Brazil (Nasif et al., 2000). In 1935 the presence of *Toxodon platensis* was reported in Agua Viva del Totumo, Lara State, from sediments of probable Pleistocene age

(Schaub, 1935). In 1937 toxodontids were also reported from the localities of El Totumo, San Miguel and El Zanjón de la Represa, north of Barquisimeto, Lara State (Nectario María, 1938).

During 1938 and 1939 George Gaylord Simpson excavated the San Miguel locality, in Lara State. He considered the fauna to be Pleistocene in age, and reported remains of Edentata, Notoungulata and Proboscidea, which are deposited in the American Museum of Natural History, New York, USA (Van Frank, 1957). Later, Van Frank (1957) referred the toxodontids (Notoungulata) from Venezuela to a different genus, named the material from San Miguel as a new genus and species, *Mixotoxodon larensis*, and also reported the age to be probably Pleistocene, but the actual age is still unknown.

Shortly thereafter, Royo y Gómez (1960) reported *Toxodon platensis* from Muaco locality, Falcón State, but did not comment on Van Frank (1957) taxonomic revision. This was corrected by Bocquentin-Villanueva (1979), who reviewed the material collected by Royo y Gómez (1960) and indicated that the toxodontids from Muaco belong to *Mixotoxodon larensis*, and commented on the existence of an indeterminate toxodontid that was similar to *M. larensis*, from

San Miguel, Lara State. The Muaco locality is late Pleistocene in age, dating between 14000 and 17000 years ago (Cruxent, 1961).

An additional middle or late Pleistocene record of *Mixotoxodon* cf. *M. larensis* was reported from Zumbador Cave, Falcón State, by Rincón (2004). The last record of *M. larensis* comes from the Plio-Pleistocene of El Breal de Orocual, Monagas State, Venezuela (Rincón et al., 2009). The present notes document new remains of *Mixotoxodon larensis* from Mene de Inciarte, in the foothills of the Sierra de Perijá, Zulia State, western Venezuela, with a preliminary discussion about paleoecological and biogeographical aspects of this species.

Institutional abbreviations. MBLUZ-P: Museo de Biología de la Universidad del Zulia, Sección de Paleontología, Maracaibo, Venezuela. VF: Museo Royo y Gómez, Universidad Central de Venezuela, Caracas, Venezuela. AMNH: American Museum of Natural History, New York, NY, USA. UF FMNH: Florida Museum of Natural History, Gainesville, FL, USA.

Terminology. Dental dimensions and terminology of Madden (1990), and Toxodontidae taxonomy of Saint-André (1999) are followed.

KEYWORDS / Mammals / Mene de Inciarte / *Mixotoxodon* / Tar Pits / Venezuela /

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Description of the Locality

The Mene de Inciarte Tar Pit is located in Mara Municipality, near the Cachirí River at the base of the Sierra de Perijá foothills, Zulia State, Venezuela (Figure 1). The area currently belongs to the Caribeña Zuliana biogeographic province (Linares, 1998). The local vegetation is dominated by *Byrsonima crassifolia* (Rincón, 2005). Logging associated with cattle ranching has resulted in loss of most of the original primary deciduous forest surrounding Inciarte, and currently only a few tall trees can be seen.

Surface exposure of tar at Mene de Inciarte extends ~1000m in NE-SW direction, with a maximum width of 500m. The presence of Pleistocene terraces developed along the margins of the area indicates that the tar seep was flooded at least once during the Pleistocene (Urbani and Galarraga, 1991).

This new fossil vertebrate assemblage was recovered from a test-pit excavation that includes 46 bird species (Steadman and Rincón, 2007); bats (Czaplewski *et al.*, 2005); canids (Prevosti and Rincón, 2007); saber tooth cats (Rincón, 2006); equids (Rincón *et al.*, 2006); armadillos, pampatheres, glyptodonts (Rincón *et al.*, 2008); ground sloths, camelids, mastodonts (McDonald *et al.*, 1999); and nine rodent species (Rincón, 2005). This fossil deposit was dated between 25.5 ± 0.6 and 27.98 ± 0.37 KaBP by accelerator mass spectrometry, using collagen extracted from Xenarthra osteoderms (Jull *et al.*, 2004). The fauna assemblage suggests that the environment during deposition of the lower levels was a savanna with isolated trees, while during deposition of the middle level it was dominated by a more humid climate, with a more compact vegetation (Rincón, 2005). Three stratigraphic levels were identified in a 1.3m deep test-pit excavation. The upper 25cm was composed of very fine sediments, without liquid tar or fossils. The middle level extended to a depth of 95cm below the surface and was composed of 80% tar and 20% sand, and contained many fossils. The lower level had a higher proportion of sand and fluid asphalt and contained large fossil bones (Rincón, 2005).

Systematic Paleontology

- Notoungulata Roth, 1903
- Toxodontia Owen, 1858
- Toxodontidae Gervais, 1847
- Haplodontheriinae Kraglievich, 1934 *sensu* Madden 1990
- Mixotroxodon* Van Frank, 1957
- Mixotroxodon larensis* Van Frank, 1957

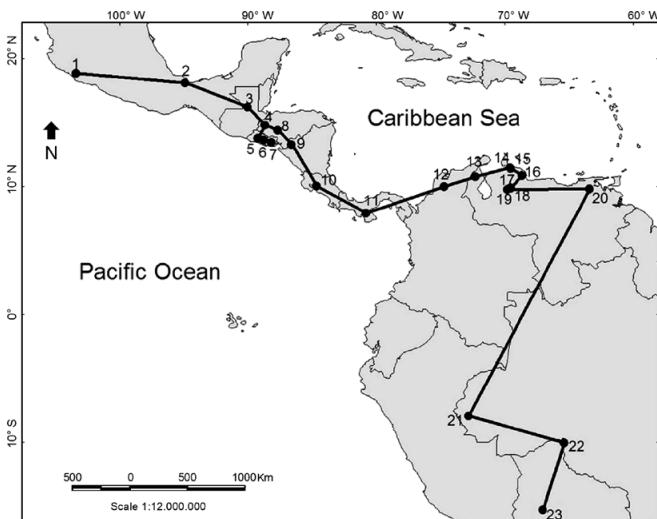


Figure 1. Geographic distribution of *Mixotroxodon larensis* in Central and South America. México: 1) Hihuitlán, Michoacan State; 2) La Esteriba, Veracruz State. Guatemala: 3) Santa Amelia River, Petén department. Honduras: 4) Yeroconte, Lempira department. 8) Orillas del Humuya, Comayagua department. El Salvador: 5) Tomayate, San Salvador department; 6) Barranca del Sisimico, San Vicente department; 7) Hormiguero, San Miguel department. Nicaragua: 9) El Bosque, Estelí department. Costa Rica: 10) Bajo de los Barrantes, Alajuela province. Panamá: 11) Ocú, Herrera province. Colombia: 12) Chivolo, Magdalena department. Venezuela: 13) Mene de Inciarte in Zulia State; 14) Muaco, 15) Ocando, and 16) Cerro Misión, in Falcón State; 17) Agua Viva del Totumo; 18) San Miguel; and 19) El Tocuyo in Lara State; 20) El Breal de Orocuá, Monagas State. Brazil: 21) Juruá River, Acre State; 22) Araras/Periquitos Rondonia State. Bolivia: 23) Cara Cara, Beni department.

Referred material (Figures 2a-h). MBLUZ-P-3.990: right mandibular ramus with m1, m2 and m3. MBLUZ-P-3.912: m1 lacks trigonid; left mandibular fragment with talonid of m3. MBLUZ-P-4.172: right mandibular fragment with alveolus for p4 and p3. MBLUZ-P-4.690: left m1 preserving the posterior crescent, talonid. MBLUZ-P-5.896: left m1 with mandibular fragments. MBLUZ-P-2.335: right i3 with medial surface broken.

Description: The alveolar border of the teeth in the mandible (MBLUZ-P-3990, Figure 2f) is parallel with the inferior margin of the horizontal mandibular ramus; there is a relatively large mentonian foramen under the alveolus for the trigonid of m1, which extends anteriorly to the posterior part of the p4 talonid. In general, i3 is procumbent like a small tusk, and incisors and molars both are ever growing without roots (hard hypsodonty); enamel disposed like a discontinuous vertical bands.

The i3 (MBLUZ-P-2.335; Figures 2c and d) is triangular in transverse cross section and curves obliquely towards the lateral side of the head; in the labial and medial sides the specimen is convex, whereas the lingual side it is concave; the medial side and its angles lack enamel band, the labial and lingual side has a wide enamel

band, which is connected in the external angle and forms a continuous enamel band, interrupted in the medial side. Close to the postero-medial angle, the enamel band of the lingual side is slim. The wear surface is worn obliquely, to ~45°.

The m1 (MBLUZ-P-3.990, MBLUZ-P-5.896, MBLUZ-P-4.690; Table I; Figure 2f) has an anteriorly projected paraconid without enamel band; a metaconid enamel band is present; metaentoconid fold shallow and reflected 45° anteromesialy; ento-hypoconid fold deeper and less inclined (85°) anteromesialy than meta-entoconid fold; hypoconid buccolingually broad, looks like a trigonid size; anterior facet of the trigonid convex; the lingual enamel band extends to the metaconid to the anterolingual side of the hypoconid, without covering it totally; buccal enamel fold deeper; buccal enamel band covering the anteromesial protoconid

facet through posteromesial hypoconulid facet; hypoconid lingually projected; buccal enamel broader than lingual enamel.

The m2 paraconid (MBLUZ-P-3.990; Table I; Figure 2f) is not anteriorly projected and lacks a meta-entoconid fold; metaconid smaller than m1 metacoonid and is covered by the lingual enamel band, which is going to the anterobuccal hypoconid edge; ento-hypoconid fold reflected 85° anteromesialy; hypoconid buccolingually broad, looks like a trigonid size; anterior facet of trigonid convex; lingual enamel band extends between metaconid to anterolingual side of hypoconid, without covering it totally; buccal enamel fold deeper; buccal enamel band covering the anteromesial protoconid facet through posteromesial hypoconulid facet; hypoconid lingually projected; buccal enamel broader than lingual enamel.

The m3 paraconid (MBLUZ-P-3.990, MBLUZ-P-3.912; Table I; Figure 2f) is not anteriorly projected; metaentoconid fold is represented as a shallow canal; metaconid covered by the lingual enamel band, which is going to the anterobuccal hypoconid edge; lacks ento-hypoconid fold; buccolingually narrow hypoconid, narrower than m1 and m2; anterior facet of trigonid convex; lingual enamel band extends between metaconid to anterolingual side of hypoconid, without covering it total-

ly; buccal enamel fold deeper than labial folds; buccal enamel band covering the anteromesial protoconid facet through posteromesial hypoconulid facet; hypoconid posteriorly projected; buccal enamel broader than lingual enamel. Talonid longer than in m1 and m2.

Paleogeographic Distribution

The paleogeographic distribution of *Mixotoxodon larensis* is presented in Figure 1, the geographic coordinates and references for the different locations being: México: 1) Huitlán, Michoacan State ($18^{\circ}52'30.00''N$ - $103^{\circ}24'14.00''W$); 2) La Estribera, Veracruz State ($18^{\circ}06'28.00''N$ $94^{\circ}53'13.00''W$) (Polaco *et al.*, 2004). Guatemala: 3) Santa Amelia River, Petén department ($16^{\circ}12'51.05''N$ - $89^{\circ}59'59.03''W$; Woodburne, 1969). Honduras: 4) Yeroconte, Lempira department ($14^{\circ}49'31.30''N$ - $88^{\circ}39'22.24''W$; Webb and Perrigo, 1984); 8) Orillas del Humuya, Comayagua department ($14^{\circ}24'35.90''N$ - $87^{\circ}39'35.12''W$). El Salvador: 5) Tomayate, San Salvador department ($13^{\circ}47'06.13''N$ - $89^{\circ}10'52.10''W$; Cisneros, 2005); 6) Barranca del Sisimico, San Vicente department ($13^{\circ}39'00.01''N$ - $88^{\circ}44'48.18''W$); 7) Hormiguero, San Miguel department ($13^{\circ}28'25.22''N$ - $88^{\circ}09'28.07''W$; Webb and Perrigo, 1984). Nicaragua: 9) El Bosque, Estalí department ($13^{\circ}18'09.97''N$ - $86^{\circ}33'35.62''W$; Leidy 1886). Costa Rica: 10) Bajo de los Barantes, Alajuela province ($10^{\circ}03'47.88''N$ - $84^{\circ}37'38.47''W$; Laurito, 1993; Valerio, 1939; Spencer *et al.*, 1997). Panamá: 11) Ocú, Herrera province ($7^{\circ}55'10.56''N$ - $80^{\circ}46'18.09''W$; Gazin, 1956). Colombia: 12) Chívolo, Magdalena department ($10^{\circ}00'49.13''N$ - $74^{\circ}40'16.76''W$; Porta 1959; Villarroel and Clavijo, 2005). Venezuela: 13) Mene de Inciarte in Zulia State ($10^{\circ}47'42.60''N$ - $72^{\circ}14'20.80''W$; this report; 14) Quebrada Ocando ($11^{\circ}25'19.03''N$ - $69^{\circ}29'34.96''W$; Bocquentin-Villanueva, 1984), 15) Muaco ($11^{\circ}28'54.08''N$ - $69^{\circ}32'39.61''W$; Royo y Gómez, 1960; Bocquentin-Villanueva, 1979) and 16) Cerro Misión ($10^{\circ}51'26.55''N$ - $68^{\circ}36'41.36''W$; Rincón, 2004), in Falcón State; 17) Agua Viva del Totumo ($9^{\circ}54'18.32''N$ - $69^{\circ}30'05.50''W$; Karsten 1886), 18) San Miguel ($9^{\circ}52'09.39''N$ - $69^{\circ}30'53.89''W$; Van Frank 1957), 19) and El Tocuyo ($9^{\circ}47'16.34''N$ - $69^{\circ}46'48.48''W$), in Lara State; 20) El Breal de Orocual, in Monagas State ($9^{\circ}50'48.3''N$ - $63^{\circ}19'46.0''W$; Rincón *et al.*, 2009). Brazil: 21) Juruá River, Acre State ($7^{\circ}54'12.57''S$ - $72^{\circ}48'09.17''W$; Paula Couto,

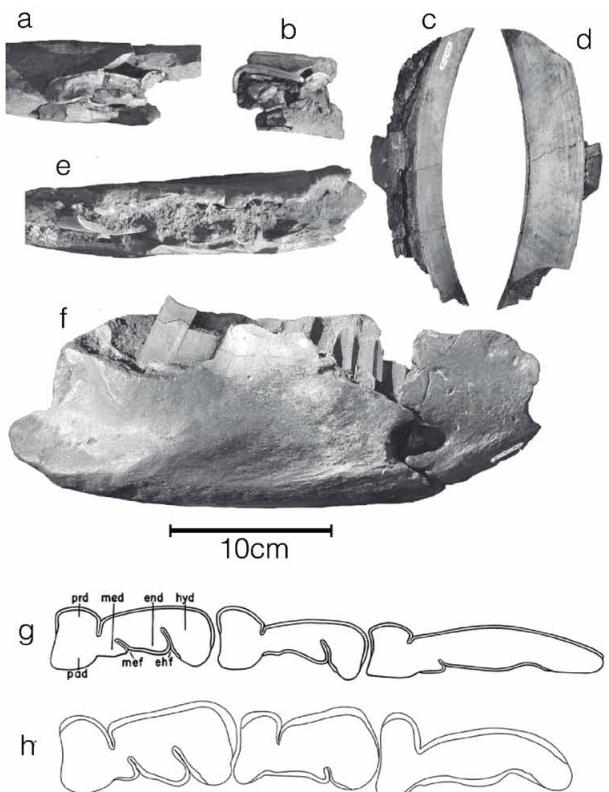


Figure 2. Teeth and lower jaw remains of *Mixotoxodon larensis* from Mene de Inciarte. a: third lower molar (MBLUZ-P-3912); b: first lower molar (MBLUZ-P-5896); c: lingual and D: labial view of the third lower incisor (MBLUZ-P-2335); e: occlusal view of the molar series of *Mixotoxodon larensis* (MBLUZ-P-3990); f: lower jaw (composed), (MBLUZ-P-4172 and MBLUZ-P-3990); g: occlusal outline of lower molar series of *Mixotoxodon larensis* from San Miguel after Van Frank 1954; and H, Mene de Inciarte (MBLUZ-P-3990). Abbreviations. ehf: ento-hypoconid fold, end: entoconid, hyp: hypoconid, med: metaconid, mef: meta-entoconid fold, pad: paraconid, prd: protoconid.

1982; Rancy, 1981), 22) Araras/Periquitos, Rondonia State ($65^{\circ}19'31.00''S$ - $10^{\circ}03'01.00''W$). Bolivia: 23)-Cara Cara, Beni department ($15^{\circ}14'19.98''S$ - $66^{\circ}59'39.95''W$; (Hoffstetter, 1968).

Discussion

Higher systematic placement of the material from Mene de Inciarte, Zulia State, Venezuela, to Toxodontidae is supported by apomorphic characters preserved on the teeth. The crescent-shaped lower molars are divided into an asymmetrical anterior portion (trigonid) and a longer, symmetrical posterior portion (talonid) with an isolated transverse crest representing the entoconid. These features diagnose the specimens as members of Notoungulata (Simpson, 1948; Lavocat, 1958; Paula Couto, 1979). A shallow sulcus (or hypoflexid) separating the trigonid and talonid permits placement in the Toxodontia (Cifelli 1993). Hard hypsodonty of the cheek teeth and tusk-like development of the i3 are diagnostic of Toxodont-

idae.

There is considerable disagreement about the finer-scale taxonomic categories within Toxodontidae. Five subfamilies were recognized by Madden (1990) based on what he considered to be diagnostic features of the teeth. These features were considered to be homoplastic by Nasif *et al.* (2000), who recognized only two subfamilies (Toxodontinae and Nesodontinae). This higher-level taxonomic ambiguity remains unsolved, and dental characters of *Mixotoxodon* itself are not well established, regardless of the subfamily to which it might be referred by varying authors (e.g. Madden, 1990; Saint-André, 1993). *Mixotoxodon* was named based on material from San Miguel, Lara State, Venezuela, the lower dentition of which appeared to represent a mixture of characters of two purported subfamilies (Van Frank, 1957). The presence of a well-developed meta-entoconid fold on m1 (suggesting affinity with Toxodontinae) and reduction or absence of the meta-entoconid fold on m2 (suggestive of Haplodontheriinae) served as part of the diagnosis for the new genus (Van Frank, 1957; Figure 2g).

The regular condition in *Mixotoxodon* m2 is lacking meta-entoconid fold, and sometimes this structure is lightly developed (Van Frank, 1957; Saint-André, 1999; Figures 2g, h), but a survey of the known m2 specimens of *Mixotoxodon* reveals interesting patterns of variation in expression of the meta-entoconid fold (anterior fold of Madden, 1997, and Nasif *et al.*, 2000). It is weakly developed in *Mixotoxodon larensis crassafonti* from Colombia (Porta, 1959), absent in the materials from Costa Rica (Laurito, 1993) and absent in the new material from Mene de Inciarte. The meta-entoconid and ento-hypoconid fold in *Toxodon* genus is well developed in m1 and m2 (Pascual, 1957). The morphological and metric (Table I) variation in this character in *Mixotoxodon* could be interpreted as individual, ontogenetic and wear related.

The Mene de Inciarte material displays the meta-entoconid fold in m1, but it is absent in m3; the ento-hypoconid fold is present in m1 and m2, but is lacking in m3. This combination of these

TABLE I
MEASUREMENTS OF FIRST, SECOND AND THIRD LOWER MOLARS OF *Mixotoxodon larensis*, *Toxodon platensis* AND *Toxodon* sp. FROM DIFFERENT LOCATIONS*

Tooth	Catalog number	Mesiodistal crown length	Breadth of the trigonid/anterior crescent	Breadth of the entolophid	Length of the trigonid/anterior crescent	Length of the talonid/posterior crescent	Length of the lingual enamel band	Paraconid/metaconid length
First lower molar	MBLUZ-P-3.990	48.8	22.5	22.1	15	32	25.5	36
	MBLUZ-P-5.896	48.8	22.8	22.7	16.8	33.5	25.6	21.8
	MBLUZ-P-4.690	-	-	16.6	-	29.9	20.2	-
	AMNH-48851	53.7	20.4	16.2	14.4	37.5	19.8	20.4
	AMNH-48852	49.6	20.4	15.6	14.1	35.8	16.2	23.5
	AMNH-55778	49.5	21.6	16.8	15.2	34.1	33.4	22
	VF-385	37.7	16.7	13.1	12.6	25.7	26.1	16.4
	VF-387-115	-	-	14.2	-	28.9	25.8	-
	AMNH-11170	41.6	18	13.9	14	27	23	21.3
	MBLUZ-P-3.990	44.3	26.6	22.5	14.4	31.7	28.8	32.7
Second lower molar	AMNH-48851	50.7	21.3	13.8	17.3	34.8	24.8	22.4
	AMNH-48864a	47.6	19.1	15	15	33.3	25.3	20.7
	AMNH-48852	48.6	20.9	14.2	15	33.1	25.4	20.9
	AMNH-116948	48	23.3	15.6	14.5	33.6	31.6	20.8
	AMNH-55777			15.6		33.3	19	
	VF-380	46.5	20	16.8	16.5	31.8	29	-
	AMNH-11170	44	20.5	12.5	16.7	27.3	25.9	24.7
Third lower molar	MBLUZ-P-3.990	61.3	23.6	17.2	14	47.4	34.2	24.1
	MBLUZ-P-3.912	60.6**	19.6**	16.6	18.2**	46.8	34.5	23.9**
	AMNH-48851	72.8	18.6	14.2	15.8	53.3	38.8	23.6
	AMNH-48852 VF-386	85 -	18.6 16.2	-11.2	15 11.6	70 -	--	-16.2
	UF-17733	63.2	18.9	12.8	13.7	47.8	36.5	21.7
	AMNH-11170	59.5	18.8	12.8	15.5	42	40	30.5
	UF-172111	59.8	16.4	12.9	13	46	44.5	22.4

* Measurements of first lower molar (m1) from Mene de Inciarte, Zulia State (MBLUZ-P-3.990; MBLUZ-P-5.896; MBLUZ-P-4.690), San Miguel, Lara State (AMNH-48851; AMNH-48852), Muaco, Falcón State (VF-385; VF-387-115) from Venezuela; Juruá River from Brazil (AMNH-55778); and *Toxodon platensis* from Argentina (AMNH-11170). Measurements of second lower molar (m2) of *Mixotoxodon larensis* from Mene de Inciarte, Zulia State (MBLUZ-P-3.990), San Miguel, Lara State (AMNH-48851; AMNH-48864a; AMNH-48852), Muaco, Falcón State (VF-380) from Venezuela; Juruá River from Brazil (AMNH-55777); Cara-Cara from Bolivia (AMNH-116948); and *Toxodon platensis* from Argentina (AMNH-11170). Measurements of third lower molar (m3) of *Mixotoxodon larensis* from Mene de Inciarte, Zulia State (MBLUZ-P-3.990; MBLUZ-P-3.912), San Miguel, Lara State (AMNH-48851, AMNH-48852); Muaco, Falcón State (VF-386) from Venezuela; Orillas del Humuya (UF-17733) from Honduras; *Toxodon platensis* from Argentina (AMNH-11170); and *Toxodon* sp. from Bolivia (UF-172111).

** Approximate measurements.

features indicates that this material belongs to *Mixotoxodon larensis* Van Frank 1957.

The Mene de Inciarte specimens are associated with a third lower incisor (i3, MBLUZ-P-2335), in which the enamel band is continuous from the lingual to the labial side, and is lacking on the mesial side, grow up curve runs linguo-labially and is concave in the mesial side. This morphology is similar to the isolated i3 (AMNH 48856, 48864g, 95755, and 39551) collected by G.G. Simpson in San Miguel, Venezuela, the i3 collected in Nicaragua by Leidy (1886) and the i3 reported by Paula Couto (1956) from Brazil (Acre), but is different from *M. larensis*, where the enamel band is isolated on the lingual side, is narrower than on the labial side and is lacking on the mesial side, grow up curve mesially in shape, but is straight labially and slightly convex lingually (AMNH 48854;

VF-383; Van Frank, 1957; Laurito, 1993; Nasif *et al.*, 2000).

Van Frank (1957) considered the i3 specimens from Venezuela (San Miguel, AMNH-48856), Nicaragua (El Bosque, ANSP 12110) and Brazil (Acre region) close to *Toxodon platensis*, possibly a geographic race, but not *M. larensis*. Nasif *et al.* (2000) and Bocquentin-Villanueva (1979) suggested that in *Toxodon* the lingual enamel band in i3 is variable, and could be continuous, wider, as wide or narrower than the labial enamel. Actually *Toxodon platensis* (AMNH 11169 and 11170) has the same i3 shape and enamel distribution of the i3 from Mene de Inciarte, but in *T. platensis* the metaentoconid and ento-hypoconid folds are present in all the molars.

The enamel band distributions of i3 specimens from Mene de

Inciarte and San Miguel, Venezuela (AMNH 48856, 48864g, 95755 and 39551) were found in stratigraphic association with molars showing *M. larensis* morphology, but these teeth were not associated with a single jaw. Because no other molar morphology was found in either locality, it can be suggested that this morphological association could be the result of intraspecific variation. Madden (1990) interpreted the discontinuity in size and morphology in *Pericotoxodon platignatus* as a sexual dimorphism; for the same reason, big differences can be present in metric and morphological features in the tusk with the same molar morphology. In any case the possibility of sexual dimorphism suggested by the Mene de Inciarte and San Miguel *M. larensis* specimens is tentative, and must await discovery of adequate additional material.

Another significant feature in the *M. larensis* material from Mene de Inciarte is the meta-entoconid fold in m3, which appears as a smooth and shallow undulation. This morphology is similar to the Costa Rica m3 (Laurito, 1993), which is different in the San Miguel *M. larensis* m3 material, where the meta-entoconid fold is marked as a slight fold. Because both morphologies of m3 are always associated with the typical m1 and m2 morphology of *M. larensis*, they could represent another intraspecific variant, but this hypothesis also requires new material before it can be rigorously tested.

Paleoecology Remarks

Mixotoxodon has been considered to be a grass/low shrub browser like *Toxodon*, and is thought to have inhabited savanna environments during the late Pleistocene (Janzen and Martin, 1982; Rancy, 1999). Certainly, the teeth are high-crowned and ever-growing, but recent isotope analyses of both genera suggest a new hypothesis about their feeding niche (MacFadden, 2005). In contrast to the conventional interpretation of *Toxodon* as a semi-aquatic savanna herbivore, Shockley (2001) interpreted the femoral locking mechanism to indicate a more terrestrially-adapted species that perhaps foraged in open-country grassland, which indicates that economic standing may be more important for ungulate herbivores.

The *M. larensis* diet is insufficient, but carbon isotope data from El Hatillo locality, Panamá, suggest that it is best interpreted to represent a canopy forest habitat (MacFadden, 2005). The feeding habitat of *Mixotoxodon* from the Orillas del Humuya, Honduras, local fauna was interpreted as a C3 forest, possibility with periods of arid stress, and also with the presence of C4 grassland (MacFadden, 2005). These data indicate that this species could live in woodland zones or probably seasonally dry forest, which are tree-dominated ecosystems with a more or less continuous canopy and grasses in minor proportion.

The distribution of *M. larensis*, on the basis of published records, is restricted to between 18°N and 15°S, which indicates an intertropical distribution for this species. Also, this species is not geographically overlapping with the more southern genus *Toxodon*. However, there are serious doubts about the taxonomy of the Acre and Cara Cara material, because these specimens are represented only by isolated teeth and thus are not highly diagnostic.

Conclusions

New remains of *Mixotoxodon larensis* are reported from Mene de Inciarte asphalt seeps, Zulia State, Venezuela. The meta-entoconid fold is lacking in m2 and m3, but is present in m1. The ento-hypoconid fold is present in m1 and m2, but is lacking in m3. The new specimens with these morphology were found in stratigraphic association with a third lower incisor that is different from previous descriptions of the i3 in *M. larensis*, because it has a continuous enamel band between lingual and labial sides. This combination of different morphologies of i3 associated with molars with typical *M. larensis* morphology is interpreted as evidence for intraspecific variation

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NUEVOS RESTOS DE *Mixotoxodon larensis* Van Frank 1957 (MAMMALIA: NOTOUNGULATA) DEL POZO DE ASFALTO DE ICIARTE, NOROESTE DE VENEZUELA

Ascanio D. Rincón

RESUMEN

Mixotoxodon larensis fue un mamífero parecido al rinoceronte moderno, el cual representa el más norteño de los toxodontes del Pleistoceno, y sus restos han sido hallados en varias localidades de Centro y Sur América. Biogeográficamente, *M. larensis* es un taxón intertropical puesto que sus registros van

desde 15°S (Bolivia) hasta 8°N (Méjico). Se reporta un nuevo hallazgo para esta especie en el pozo de asfalto del Mene de Iciarte, Sierra de Perijá, Estado Zulia, Venezuela, con una edad estimada en 25-27000 años (Pleistoceno Tardío).

NOVOS RESTOS DE *Mixotoxodon larensis* Van Frank 1957 (MAMMALIA: Notoungulata) DO POÇO DE ASFALTO DE ICIARTE, NOROESTE DA VENEZUELA

Ascanio D. Rincón

RESUMO

Mixotoxodon larensis foi um mamífero tipo Rhinoceronte moderno, que representa o mais nôrdico dos toxodontes do Pleistoceno, e seus restos tem sido encontrados em varias localidades do Sul e Centro América. Biogeográficamente, *M. larensis* é uma taxa intertropical posto que seus registros vão desde 15°S (Bolívia)

até a 8°N (Méjico). Aqui se informa um novo registro para esta espécie no poço de asfalto de Iciarte, Sierra de Perijá, Estado Zulia, Venezuela, com uma idade estimada em 25-27000 anos (Pleistoceno Tardio)