



# MESOTHERIID (MAMMALIA, NOTOUNGULATA) REMAINS FROM THE COLHUEHUAPIAN BEDS (EARLY MIOCENE) OF CHICHINALES FORMATION, RÍO NEGRO PROVINCE, ARGENTINA

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<sup>3</sup>CONICET

THE Mesotheriidae represent one of several clades of the endemic South American ungulate Order †Notoungulata. This clade has some rodent-like adaptations such as hypertrophied upper and lower incisors, highly hypsodont cheek teeth, reduced dental formula (in younger forms), simplified occlusal morphology, and specialized zygomaseteric structure, among other features (Patterson, 1934; Billet *et al.*, 2008). Traditionally, the Mesotheriidae have been divided into two subfamilies: Trachytheriinae and Mesotheriinae (Simpson, 1945). Recent phylogenetic analyses supported the monophyly of Mesotheriinae, but indicated that Trachytheriinae is a paraphyletic assemblage of basal mesotheriids (Cerdeño and Montalvo, 2001; Croft *et al.*, 2004; Reguero and Castro, 2004; Billet *et al.*, 2008).

The Mesotheriidae comprise younger forms persisting until the Ensenadan SALMA (early–middle Pleistocene) (Ameghino, 1906). Until recently, the Mesotheriinae were supposed to have appeared in the middle Miocene (Friasian *sensu lato*), being absent in the early Miocene Colhuehuapian and Santacrucian SALMAs (Simpson, 1940; Marshall *et al.*, 1983; Bond, 1986). The recently discovered Chucal Fauna from Northern Chile (Flynn *et al.*, 2002; Croft *et al.*, 2004) containing three species of mesotheriines agrees with a Santacrucian age (Croft *et al.*, 2004).

Other basal mesotheriines were reported from other early to middle Miocene faunas. The probably early Miocene mesotheriid from the Mariño Formation, Mendoza Province (Cerdeño *et al.*, 2006; Cerdeño, 2007) was found to be similar to the Chucal species *Altitypotherium chucalensis* (Cerdeño, 2007). Additionally, "*Trachytherus? mendocensis*" (Simpson and Minoprio, 1949; Simpson *et al.*, 1962) –origi-

nally described as a trachytheriine from the Divisadero Largo Formation, Mendoza– was re-interpreted as a primitive mesotheriine more probably coming from the overlying early Miocene Mariño Formation (Cerdeño *et al.*, 2006, 2008). López *et al.* (2009) reported a new mesotheriine genus and the presence of *?Altitypotherium* from the early Miocene Chinchales Formation in San Juan Province, but this new taxon remains formally undescribed.

Herein are described the first mesotheriid remains from the Chichinales Formation in the surroundings of Paso Córdoba, on the southern bank of the Río Negro near the city of General Roca, Río Negro Province (Fig. 1). Fossils were collected from lower deposits of this 2.10 m thick unit (Barrio *et al.*, 1989; Kramarz *et al.*, 2004). The fossil fauna is Colhuehuapian in age (early Miocene) as indicated by the presence of *Colpodon* Burmeister, 1885, *Cramauchenia* Ameghino, 1902, *Willedewu* Vucetich and Verzi, 1991, *Australoprocta* Kramarz, 1998, and *Cochilius volvens* Ameghino, 1901 (Windhausen, 1922; Barrio *et al.*, 1989; Kramarz *et al.*, 2004). The geological context and stratigraphic profile of the Chichinales Formation is fully detailed in Barrio *et al.* (1989).

**Abbreviations.** MACN Pv, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; MCNAM- PV, Museo de Ciencias Naturales y Antropológicas "J. C. Moyano", Mendoza; MEGP, Museo Educativo de Geología y Paleontología de General Roca, Río Negro; MLP, Museo de La Plata; SGOPV, Museo Nacional de Historia Natural, Santiago de Chile; UATF, Universidad Autónoma Tomás Frías, Potosí,

Bolivia; **SALMA**, South American Land Mammal Age. Upper/lower tooth loci are indicated by upper/lower case letters (e.g., **M1**, **m1**).

### SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903  
 Suborder TYPOTHERIA Zittel, 1892  
 Family MESOTHERIIDAE Alston, 1876  
 Subfamily MESOTHERIINAE Simpson, 1945

#### Figuras. 2–3

**Material.** MEGP 102a, right maxillary fragment with incomplete M3; MEGP 102b and MEGP 102c, incomplete right M1 or M2; MEGP 102d, incomplete left M1 or P4; MEGP 102e, right m1; MEGP 102 f, left m2; MEGP 166 left m2. All the specimens were found isolated.

**Description.** Upper cheek teeth (Fig. 2.1–4) incomplete, ectolophs and some parts of the crown missing. Tooth crowns considerably high, even if partially broken, showing no evidence of root formation. Preserved bases of molars showing same pattern of lobes as occlusal surfaces (Fig. 3). This suggests that these teeth are euhypsodont (*sensu* Mones, 1982), as in all the mesotheriines and in contrast to the molars of Trachytheriinae (protohypsodont) in which the occlusal pattern is different from that observed at the base of the crown. All upper cheek teeth lack fosettes and a layer of cement covers the walls and fills the lingual sulci.

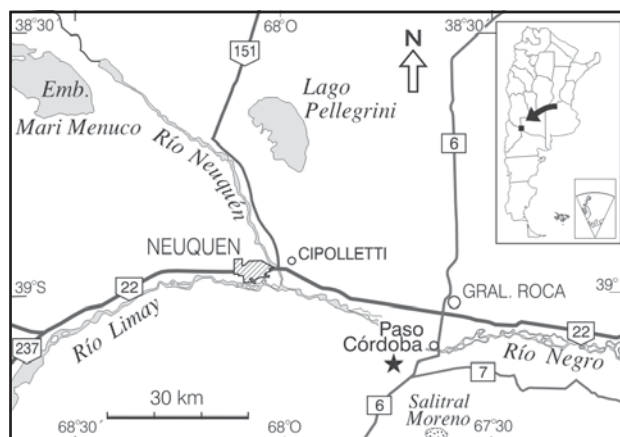
The only available M3 (MEGP 102a, Fig. 2.1) lacks the anterior part of the ectoloph, but the posterior extension of the ectoloph, known as “fourth lobe”, can be distinguished as in other mesotheriines (Francis, 1965). Specimen MEGP

102a possesses a typical mesotheriine trilobed pattern; the anterior and posterior lobes converge lingually but not enclosing the middle lobe, which almost reaches the lingual wall of the tooth; in this it is similar to *Altitypothierium paucidens* and specimen SGOPV 5156 assigned to *Eotypothe-rium chico*, both from Chucal (Croft *et al.*, 2004). On the contrary, *A. chucalensis*, the holotype of *E. chico*—also from Chucal (Croft *et al.*, 2004: fig. 11 A,)—, the M3 (MLP 45-VII-10-2) referred to “*Trachytherus? mendocensis*” from Divisadero Largo (Cerdeño, 2007), and *Altitypothierium cf. chucalensis* (MCNAM-PV 3648) from the Mariño Formation (Cerdeño, 2007) have the middle lobe of M3 fully enclosed by the other two lobes. The length of MEGP 102a (from the mesial wall to the posterior tip; Tab. 1) is slightly greater than that of *Altitypothierium paucidens* (Croft *et al.*, 2004). The distalmost part of the palate preserved in MEGP 102a shows a wide postpalatal notch not reaching the level of M3, as in the holotypes of *A. paucidens* and *E. chico*, and unlike *A. chucalensis*.

Specimens MEGP 102b and 102c (Figs. 2.3–4; Tab. 1) only preserved the lingual portions of the crown, being closer to those of *E. chico* than to the species of *Altitypothierium*. Both are euhypsodont and trilobed, but have a small, triangular middle lobe fully enclosed by the anterior and posterior lobes, but more developed than in MEGP 102d (Fig. 2.2). This condition is similar to that of M1 in *Altitypothierium chucalensis* and M1 in the specimen SGOPV 5156 referred to *Eotypothe-rium chico*. On the contrary, M2 of *A. chucalensis*, M1–M2 of *A. paucidens*, and M1–M2 of the holotype of *Eotypothe-rium chico* have the middle lobe fully developed and reaching the lingual wall.

Specimen MEGP 102d (Fig. 2.2) presents essentially a bilobate occlusal pattern with a rudimentary middle lobe represented by a minute triangular spur of the ectoloph, resulting in a Y-shaped lingual sulcus with sub-equal anterior and posterior arms. This condition is identical to that of P4 of UATF-V-000840 from the middle Miocene Fauna of Cerdas, Bolivia, described as Mesotheriinae gen. et sp. indet. (Townsend and Croft, 2010). It also resembles P4 of specimen SGOPV 5074 referred to *E. chico* (Croft *et al.*, 2004), but in this specimen the Y-shaped valley is isolated, forming a central fossette because of its more advanced ontogenetic stage. M1 of “*Trachytherus? mendocensis*” (Simpson *et al.*, 1962) also has a rudimentary, triangular middle lobe, but the anterior arm of the Y-shaped lingual sulcus is significantly longer than the posterior one.

Lower teeth MEGP 102e (Fig. 2.5), MEGP 102f, and



**Figure 1.** Geographic location of the fossiliferous locality/ Ubicación geográfica de la localidad fosilífera

MEGP 166 (Fig. 2.6) are similar in morphology. They have a completely open base and lack fossettids. The trigonid and talonid are rounded; the trigonid has a straight anterior border without enamel. The labial sulcus is narrow and deep, almost reaching the lingual wall, and slightly oriented posterolingually. A shallow lingual sulcus is opposed to the labial sulcus. A layer of cement covers the lingual, labial, and distal faces. These teeth do not show significant morphological differences with those of other Miocene mesotheriines. The size of MEGP 102f and MEGP 166 is similar to that of species of *Altityotherium*, whereas the size of MEGP 102e falls into the size distribution of *E. chico* (Tab. 1).

### DISCUSSION AND CONCLUSIONS

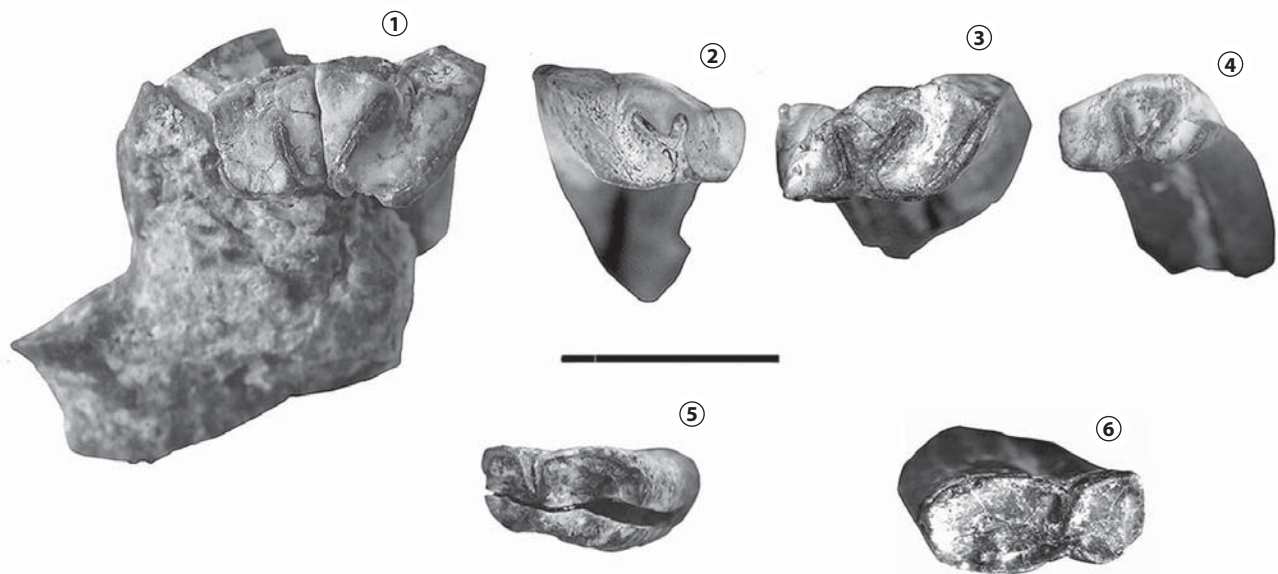
The assignment of these specimens to the Subfamily Mesotheriinae is based on the absence of fossettes and fossettids, the degree of hypsodonty, and the presence of a persistent middle lobe in upper molars. Other synapomorphies of the clade (Cerdeño and Montalvo, 2001; Croft *et al.*, 2004) cannot be checked because of the fragmentary nature of the material.

The cheek-teeth from Chichinales are continuous growth teeth, with no signs of ontogenetic variations, as the bases of the molars bear the same pattern of lobes as the occlusal surface (Fig. 3). The same condition is observed in other basal mesotheriines, such as the yet undescribed specimens

from the Chinchas Formation (San Juan) (M.B., pers. obs.) and M3 (MLP 45-VII-10-2) of “*Trachytherus? mendocensis*” (Simpson *et al.*, 1962). Similarly, the molars of the Chucal mesotheriines show no morphological variations attributable to wear (D. Croft, pers. comm.). Only M1 of the Mariño mesotheriine shows a slight difference between both extremities of the crown (Cerdeño, 2007, p. 770). The absence of ontogenetic variations in the molars of the specimens from Chichinales appears to be a condition shared by most of the early-diverging mesotheriines.

Accordingly, the significant differences in occlusal morphology—especially in the middle lobe—among the upper molars from Chichinales are here interpreted as possibly a result of different positions in the tooth-row and less probably to taxonomic differences. The specific assignment of the isolated teeth is uncertain and highly speculative, given the scarcity of the available remains.

Specimen MEGP 102d stands out by having a poorly developed middle lobe resulting in a Y-shaped lingual sulcus. This feature has only been observed in M1 of the holotype of the putative mesotheriine “*Trachytherus*” *mendocensis* (Cerdeño *et al.*, 2008) and in P4 of two other mesotheriines, one from Chucal in Chile (Croft *et al.*, 2004) and the other from Cerdas in Bolivia (Townsend and Croft, 2010). In the former, the Y-shaped lingual sulcus is ephemeral (Croft *et al.*, 2004), and in the latter this condition is unknown.

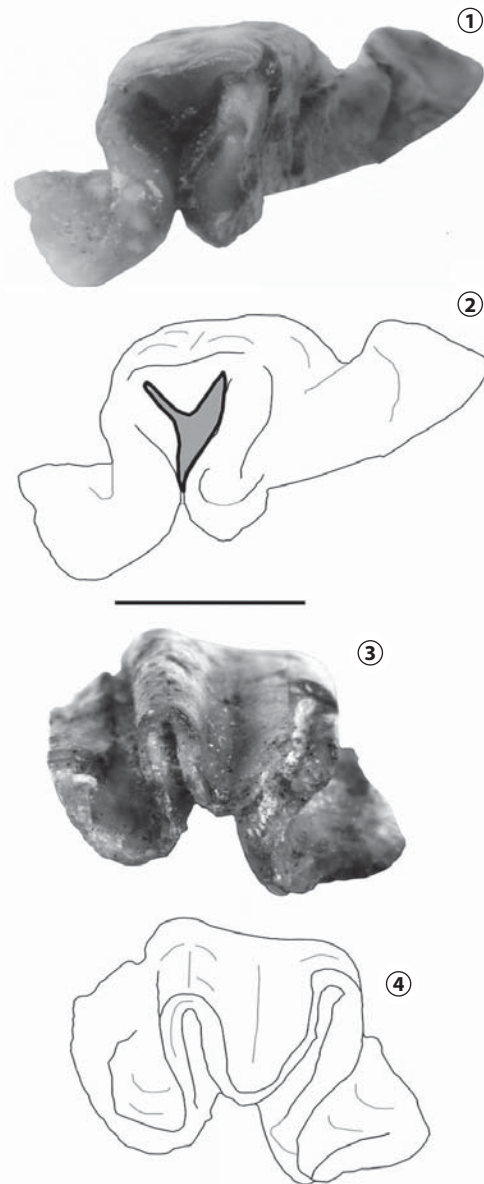


**Figure 2.** Mesotheriinae from Chichinales Formation. **1**, MEGP 102a, incomplete right M3; **2**, MEGP 102d, incomplete left M1 or P4; **3**, MEGP 102c, incomplete right M1 or M2; **4**, MEGP 102b, incomplete right M1 or M2; **5**, MEGP 102e right m1; **6**, MEGP 166 left m2. Labial to top. Scale bar. / *Mesotheriinae de la Formación Chichinales*. **1**, MEGP 102a, M3 derecho incompleto; **2**, MEGP 102d, M1 o P4 izquierdo incompleto; **3**, MEGP 102c, M1 o M2 derecho incompleto; **4**, MEGP 102b, M1 o M2 derecho incompleto; **5**, MEGP 102e m1 derecho; **6**, MEGP 166 m2 izquierdo. Labial hacia arriba. Escala = 10 mm.

Therefore, if MEGP 102d is a premolar, it represents the first one known to show –among mesotheriines– a permanent Y-shaped lingual sulcus. The possibility of MEGP 102d being a dP4 is rejected because in mesotheriines this tooth has an ephemeral middle lobe (Patterson, 1952; Francis, 1965). If MEGP 102d is considered an M1, its combination of a Y-shaped sulcus and euhyposodnty is also unique among mesotheres. M1 of “*Trachytherus mendocencis*” has a similar Y-shaped sulcus, but the specimen is lost and the degree of hyposodnty was not described by Simpson *et al.*, (1962); therefore, this feature is uncertain. Molars of the remaining mesotheriines are positively euhyposodont, but with a more developed middle lobe. Croft *et al.* (2004, p. 17) concluded that the limited lingual exposure of the middle lobe observed in M1 of some Chucal mesotheriines is a primitive character for this group. Consequently, MEGP 102d represents a condition even more primitive than in the Chucal species, and documents an evolutionary stage not previously recorded within this clade.

Until now, the Chucal mesotheriines were considered the oldest record of Mesotheriinae. Radioisotopic dates and biostratigraphic data refer the Chucal Fauna to the Santacrucian SALMA (late early Miocene) (Croft *et al.*, 2004). The age of the Mariño Formation remains controversial. However, based on the presence of a mesotheriid close to the Chucal species and of the rodent *Scleromys* Ameghino, 1887, the middle Member of the unit is considered early Miocene, probably Santacrucian in age (Cerdeño *et al.*, 2006; Cerdeño, 2007; Cerdeño and Vucetich, 2007). Recently, Cerdeño *et al.* (2008) suggested that “*T. mendocensis*”, originally reported as coming from the Paleogene Divisadero Largo Formation, may actually come from the Mariño Forma-

tion. The faunal association from the Chinchas Formation in San Juan Province is referred to the Santacrucian SALMA (López *et al.*, 2009). Cattoi (1962) reported a trachytheriine from Tertiary sediments in central Patagonia associated with other mammals interpreted as Colhuehuapian; this material (MACN Pv 17681) probably belongs to a mesotheriine, but



**Figure 3.** View of the bases of two Mesotheriinae upper teeth from Chichinales Formation. **1**, MEGP 102d, incomplete left M1 or P4; **2**, same, line drawing; **3**, MEGP 102b, incomplete right M1 or M2; **4**, idem, line drawing. Scale bar = 5mm. / Vista de las bases de dos dientes superiores de Mesotheriinae de la Formación Chichinales. **1**, M1 o P4 izquierdo incompleto; **2**, idem, dibujo esquemático; **3**, M1 o M2 derecho incompleto; **4**, idem, dibujo esquemático. Escala = 5 mm.

**TABLE 1.** Tooth measurements (in mm) of the mesotheriines from the Chichinales Formation. Abbreviations: L, anteroposterior length; W, transverse width. \* maximum preserved length / Medidas dentarias (en mm) de los mesoteriinos de la Formación Chichinales. Abreviaturas: L, largo anteroposterior; W, ancho transverso. \* largo máximo preservado.

| Specimen                  | L    | W   |
|---------------------------|------|-----|
| MEGP 102a, right M3       | 14,7 | -   |
| MEGP 102b, right M1 or M2 | 7,0* | -   |
| MEGP 102c, right M1 or M2 | 9,2* | -   |
| MEGP 102d, left M1 or P4  | 8,6* | -   |
| MEGP 102e, right m1       | 8,4  | 5,7 |
| MEGP 102f, left m2        | 11,3 | 6,2 |
| MEGP 166, left m2         | 10,6 | 6,1 |



the supposedly associated remains—particularly the rodents—are not conclusive in relation to the age and could pertain to a younger SALMA (Santacrucian?). Consequently, the mesotheriid remains from the Chichinales Formation represent the first record of the family in beds confidently assigned to the Colhuehuapian SALMA and thus the earliest record of the Mesotheriinae.

Reguero and Castro (2004) proposed that the absence of mesotheriids in Patagonia during Colhuehuapian and Santacrucian SALMAs is probably due to retraction of the distribution area of the family, and Croft *et al.* (2003) suggested that middle latitudes of South America (Northern Chile, Bolivia) were centers of diversification of mesotheriids during the early Miocene. The Chichinales mesotheriids reveal the presence of the family in northern Patagonia during the early Miocene, suggesting that the putative geographic retraction may have affected only southern and central Patagonia.

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