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# The Pliocene pronghorn *Hexobelomeryx fricki* (Mammalia: Artiodactyla) from San Miguel de Allende, Guanajuato, central Mexico

**Eduardo Jiménez-Hidalgo[1,*] and Oscar Carranza-Castañeda[2]**

*[1] Laboratorio de Paleobiología, Instituto de Recursos, Campus Puerto Escondido, Universidad del Mar, Km. 2.5 Carretera Puerto Escondido-Oaxaca, Puerto Escondido, Oaxaca 71980, México.*
*[2] Centro de Geociencias, Universidad Nacional Autónoma de México, Campus Juriquilla, Juriquilla, Querétaro 76230, México.*
** eduardojh@zicatela.umar.mx*



## ABSTRACT

*Hexobelomeryx fricki is recorded in the San Miguel de Allende graben since the late early Hemphillian to the Blancan III, from about 7.0 million years to 3.0 million years. The studied specimens were recovered from floodplain and point bar deposits of the informal Rancho Viejo beds. The mortality profile of the H. fricki teeth sample from the study area is an attritional one, with few juveniles and a large majority of old individuals. The estimated body mass of H. fricki specimens range from around 10 to 30 kilograms, according to their age at death. The record of this pronghorn in Guanajuato during the late early Hemphillian and the Blancan III, are the oldest and the youngest occurrence of the species in North America and extends its geographic distribution from northwestern Mexico to central Mexico during the late Hemphillian.*

*Key words: Hexobelomeryx, Hemphillian, Blancan, Pliocene, San Miguel de Allende, Mexico.*

## RESUMEN

*Hexobelomeryx fricki está presente en el graben de San Miguel de Allende desde la parte tardía del Henfiliano temprano hasta el Blancano III, desde hace aproximadamente 7.0 millones de años hasta hace 3.0 millones de años. Los ejemplares estudiados fueron recolectados de depósitos de llanura de inundación y barras de punta de la unidad informal capas Rancho Viejo. El perfil de mortalidad de la muestra de dientes de H. fricki del área de estudio es atricional, con pocos individuos jóvenes y una gran mayoría de individuos viejos. La masa corporal de los ejemplares de H. fricki tiene un rango entre 10 kilogramos y 30 kilogramos, dependiendo de su edad al momento de morir. El registro de este antilocáprido en Guanajuato durante la parte tardía del Henfiliano temprano y el Blancano III, representa la ocurrencia más antigua y más reciente de la especie en Norteamérica y extiende su distribución geográfica desde el noroeste de México hasta el centro del país durante el Henfiliano tardío.*

*Palabras clave: Hexobelomeryx, Henfiliano, Blancano, Plioceno, San Miguel de Allende, México.*

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## INTRODUCTION

For more than 30 years, *Hexobelomeryx fricki* Furlong 1941 was the only antilocaprid identified in the Pliocene faunas of Mexico. The species was erected based upon specimens from the latest Hemphillian Yepómera/Rincón and Matachic local faunas of Chihuahua (Lindsay *et al.*, 2006).

In central Mexico, the specimens *Hexobelomeryx* sp. or *Hexobelomeryx* cf. *H. fricki* have been reported from the late early Hemphillian of Hidalgo state (Zietla-Tehuichila fauna) and the late Hemphillian of Jalisco state (Tecolotlán and Teocaltiche local faunas) (Montellano-Ballesteros, 1997; Carranza-Castañeda, 2006).

At San Miguel de Allende, Guanajuato, Dalquest and Mooser (1980) assigned abundant large teeth from rancho El Ocote to Antilocapridae indet., indicating that they are close in size to those of *H. fricki*. Also, several papers mention *Hexobelomeryx* sp., or *Hexobelomeryx* cf. *H. fricki* in the Hemphillian and Blancan local faunas of San Miguel de Allende (Carranza-Castañeda and Ferrusquía-Villafranca, 1978; Miller and Carranza-Castañeda, 1984; Carranza-Castañeda, 1989; Carranza-Castañeda and Walton, 1992; Miller and Carranza-Castañeda, 1998; Jiménez-Hidalgo *et al.*, 2004; Carranza-Castañeda, 2006), but up to date, no specimen has been formally described.

In the United States of America there is a record of cf. *Hexobelomeryx* sp. from the latest Hemphillian of Texas and of *Hexobelomeryx*? sp. from the late Hemphillian of Nevada (Janis and Manning, 1998).

Our study of the antilocaprid specimens recovered from Hemphillian and Blancan localities of the San Miguel de Allende area, allow us to recognize several size-groups among the diverse skeletal elements present in the collection. These size-groups are not related to the age of individuals, but represent different pronghorn species (Jiménez-Hidalgo and Carranza-Castañeda, 2004). One of these species -*Capromeryx tauntonensis*- was previously described from the Blancan localities of the study area (Jiménez-Hidalgo *et al.*, 2004).

The purpose of this paper is to describe the largest size-group of upper and lower teeth and mandibles recovered from several Hemphillian and Blancan localities of San Miguel de Allende and to discuss some paleobiological considerations about the *Hexobelomeryx* record from Guanajuato, central Mexico.

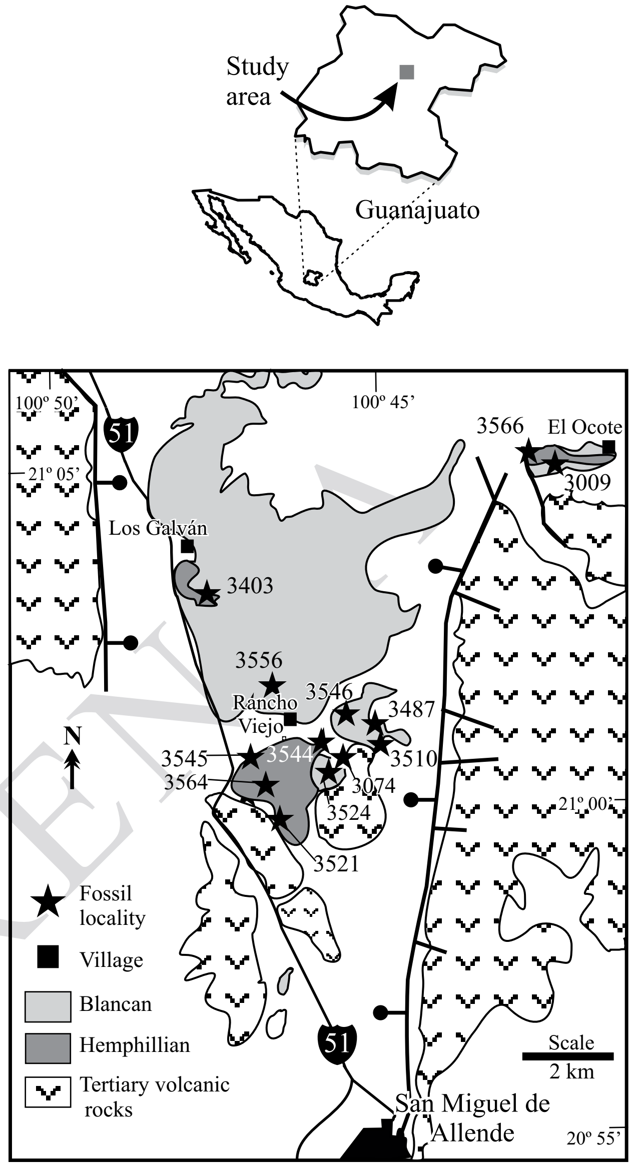


Figure 1. Index map and geologic map of the San Miguel de Allende area showing the localities where the *Hexobelomeryx fricki* specimens were collected. Geologic map modified from Adams *et al.* (2006).

## GEOLOGIC SETTING AND GEOCHRONOLOGY

The San Miguel de Allende basin is located in the northeastern part of Guanajuato state, between 20º55'- 21º06' North Latitude and 100º50'- 100º41' West Longitude W (Figure 1), in the Central Mexico Highlands.

The studied specimens were collected from clay and silty to sandy clay with variable sand, gravel and tuffaceous components, which were deposited as floodplain and point bar sequences of the informal lithostratigraphic unit named Rancho Viejo beds (Carranza-Castañeda *et al.*, 1994; Flynn *et al.*, 2005).

In this paper we used the registered numbers of the Catálogo de Localidades of the Colección Nacional de Paleontología, Museo Ma. Carmen Perrilliat M., Instituto de Geología, Universidad Nacional Autónoma de México.

Thirteen places with *Hexobelomeryx* fossils are located between 12 and 20 km north of San Miguel de Allende city (Figure 1). On five of those places, radiometric dates or magnetostratigraphic analysis were obtained by other authors (Table 1), whilst for the rest, the faunal association and stratigraphic correlations are indicative of the age of these localities (Flynn *et al.*, 2005; Adams *et al.*, 2006).

The ages of all of these localities span from the late early Hemphillian (Hh2) to the Blancan III, from around 7.0 to 3.0 Ma (Kowallis *et al.,* 1998; Flynn *et al.*, 2005; Adams *et al.*, 2006; Carranza-Castañeda, 2006).

The associated fauna recovered from the same bed where *Hexobelomeryx* specimens were collected, at locality 3545 La Presa, is assigned to the late early Hemphillian (Hh2), while the associated fauna at locality 3521 Coecillos, belongs to late (Hh3) and latest Hemphillian (Hh4). The associated fauna of locality 3544 Rancho San Martín, locality 3556 Earthwatch and locality 3566 Candado, are assigned to the late (Hh3) and latest Hemphillian (Hh4). For the same reason, the associated fauna of locality 3487 Ferrocarril 2, locality 3510 Perros Bravos and locality 3546 Cara Cara, is assigned to the Blancan III (Jiménez-Hidalgo *et al.*, 2004; Bell *et al.*, 2004; Carranza.Castañeda, 2006 and references therein; Jiménez-Hidalgo and Carranza-Castañeda 2010).

The Hemphillian and Blancan associated fauna from the same beds where the *Hexobelomeryx* material was recovered consists of diverse species of xenarthrans, lagomorphs, rodents, ursids, canids, mustelids and felids; also, ghomphotherids, rhinoceroses equids, tayassuids, a protoceratid, camelids and some other antilocaprid species have been collected (Carranza-Castañeda and Miller, 2000; Carranza-Castañeda, 2006; Jiménez-Hidalgo and Carranza-Castañeda, 2010). The mammalian index genera and species of the bearing localities from San Miguel de Allende were previously published by Carranza-Castañeda (2006) and references therein; so, they are not repeated here.

## MATERIALS AND METHODS

The fossil material described in this paper consists of isolated upper and lower cheek teeth, some maxillary fragments with teeth and rami fragments with teeth. They were collected from the surface.

The fossils were prepared at Instituto de Geología, Universidad Nacional Autónoma de México (UNAM), México City, using standard techniques. The specimens are housed at the Colección Nacional de Paleontología, Museo Ma. Carmen Perrilliat M., Instituto de Geología, Universidad Nacional Autónoma de México with the acronym IGM.

Comparisons of specimens were made with the paratypes and drawn teeth specimens of Furlong (1941) of *Hexobelomeryx fricki* housed at the Natural History Museum of Los Angeles County (LACM [CIT]).

The used dental nomenclature is that of Gentry and Hooker (1988). The measurements of upper and lower dentition were taken with a caliper as maximum lengths and widths at occlusal level (Janis, 1990). All measurements are expressed in millimetres (mm). Upper and lower teeth are represented by upper and lower case: I/i (incisor),

Table 1. Geochronology of the San Miguel de Allende localities that bear *Hexobelomeryx fricki* specimens (Data from Flynn *et al.*, 2005; Adams *et al.*, 2006).

| Locality | Radiometric date (Ma) | Chron |
|---|---|---|
| 3009 Arroyo la Carreta | 5.7 ± 0.4 to 4.8 ± 0.2 | C3n.4n?-C3n.3n |
| 3403 La Rinconada | 4.4 ± 0.3 | C3n.3n |
| 3564 Arroyo Tepalcates | | C3n.2r –C3n.2n or C3n.3r??-C3n.3n?? |
| 3074 Arrastracaballos | 3.3 ± 0.1<br>3.6 | C2An.3n |
| 3524 Porkchop | | Middle C2An.3n |

C/c (canine), P/ p (premolar), M/m (molar), D/d (deciduous tooth). Measurement abbreviations are: L, length; W, width; kg, kilogram. Additional abbreviations include: Gto, Guanajuato; Ma, million years; n, sample size; OR, observed range; FLML, first lower molar length; LMRL, lower molar row length; Pad, Probable absolute age at death; SLMA, second lower molar area; UCMP, University of California Museum of Paleontology; USA, United States of America; $\overline{X}$, sample mean; yrs, years.

Given that the stage of wear strongly correlates with the characters that can be observed on teeth and that also is related with the observed tooth crown height, it is very important to compare teeth with the same stage of wear (Breyer, 1977).

In this paper we propose the use of five tooth wear stages:

I. Deciduous premolars present, molar two erupting.

II. Permanent premolars present, M1/ m1 slight to moderately worn.

III. Worn premolars, M1/m1 heavy worn, M3 metastyle or m3 entostilid without wear.

IV. Permanent premolars and M2/m2 moderately worn, M3 metastyle or m3 entostilid slightly worn.

V. Heavy worn molars, M3 metastyle or m3 entostilid worn, both crescents tend to fuse.

In order to estimate the probable absolute age at death of the *Hexobelomeryx* specimens from Guanajuato, we used the tooth-wear scoring system proposed by Lubinski (2001) for *Antilocapra americana* (Ord, 1815), in which mandibular cheek teeth are evaluated for presence or absence of fossettids, dentine wear on ridges and continuous dentine links (see fig. 5 of Lubinski, 2001). The resulting scores were then compared with table 7 of Lubinski (2001) of tooth wear, known age and established-age specimens.

On the other hand, the body mass estimations of studied specimens were based in the ruminants' predictive equations of Janis (1990) for lower molar row length (LMRL) and second lower molar area (SLMA) as well as the multivariate body mass determination algorithms 7.2 and 7.3 of Mendoza *et al.* (2006).

## SYSTEMATIC PALEONTOLOGY

Suborder Ruminantia Scopoli, 1777
Family Antilocapridae Gray, 1866
Subfamily Antilocaprinae Gray, 1866

***Hexobelomeryx* Furlong, 1941**
***Hexobelomeryx fricki* Furlong, 1941**
Figures 2 and 3; Tables 2 – 4

**Diagnosis.** Three-tined horns with unequal, tapering tines; anterior tine shortest with other two more nearly equal; angle of divergence between tines either nearly equal or middle and posterior tine less divergent than anterior and middle; teeth hypsodont; superior cheek tooth series short; m3 with three major lobes and a small but variable fourth lobe; rami relatively short, diastema short, mandible dorsoventrally deep at m3; P4 with strong styles (Furlong, 1941; Janis and Manning, 1998), and a P4 medial rib that disappears as tooth wear increases.

**Description.** *Mandible.* The diastemal crest is sharp and its ventral border is almost straight (Figure 2). The depth of the horizontal ramus increases significantly below the m2 and m3 and its depth decreases rapidly toward the diastema (Figure 2). The masseteric ridge is well developed and the angular process is convex.

*Lower dentition.* The complete cheek teeth series is p2-m3, but in less than 9 % of the San Miguel de Allende sample there is p2 alveolus; in most of mandibles there is not sign of p2 or its alveolus.

The p3-p4 length percent regarding the m1-m3 length is around 26% to 30 % depending on the teeth wear stage (Tables 2 and 3).

In the specimens with tooth wear stage I, the dp3 is about 1/3 larger than its permanent counterpart. In the lingual portion of the dp3 there are two valleys that delimitate a width anterior enamel fold, a middle enamel fold and a well-developed posterior enamel fold. The dp4 is worn, it has three crescents of which the caudal is the larger; a posterior stylid is moderately developed (Figures 2.1 and 2.2).

The m1, in a stage of wear I, have little worn fossettids, the metaconid and entoconid are acute, the parastylid and entostylid are well developed but the metastylid is not developed. The m2 is unworn, the fossettids are deep and the parastylid and entostylid are well developed (Figures 2.1 and 2.2).

The teeth of mandible IGM 9383 show a wear stage II. Its p4 is broken anteriorly, so, it is only possible to observe that is somewhat worn; the m1 has a well-developed entostylid. The m2 is little worn, the parastylid and entostylid are well developed. The m3 is erupting, has deep fossettids, the metaconid and entoconid are acute and the parastylid is slightly worn (Figures 2.3 and 2.4).

The p3, in wear stage III, has two valleys that separate the worn stylids, the anterior one is wider than the posterior, and persist with additional wear. In the posteriolabial part there is a wide valley delimiting an enamel fold, which disappears with additional wear. The p4 is compressed, short, the paraconid is very well developed and on its caudal part there is a deep fossetid (Figures 2.5 and 2.6).

The m1 in wear stage III, has very worn fossettids, the metaconid and entoconid have little wear, the parastylid and entostylid are slightly developed. The anterior crescent is slightly smaller than the posterior one. The m2 has moderately worn fossettids, the metaconid and entoconid are acute and the parastylid and entostylid are moderately developed. The m3 have slightly worn fossettids, the metaconid and entoconid are acute and the parastylid is well developed (Figures 2.5 and 2.6).

The teeth in wear stage IV are similar to those in wear stage III, but the parastylid of p4 is wider and its posterior fossettid is shallower. In the m1 the parastylid still is present but the other stylids are lost, and both fossettids have disappeared. In the m2 the fossettids are severely worn and the entostylid is slightly developed. The fossettids of m3 are moderately worn, being that of the hypoconulid the most-worn one when compared with the other two; the parastylid is moderately to well developed and the other stylids are lost (Figures 2.7 and 2.8).

Finally, in wear stage V, the premolars have a triangular-to-ovoid outline; the molars are severely worn, they have lost the fossetids and the stylids are slightly or not developed (Figures 2.9–2.12).

*Upper dentition.* Large part of the upper teeth sample from San Miguel de Allende shows a wear stage IV or V (Figure 3), and a few can be classified in stage of wear II or III. Also, there are no upper teeth with a wear stage I.

In wear stage II the anterior fossette of M1 is well worn and the posterior one is moderately worn; the paracone and metacone are fairly acute; the parastyle is little developed but the mesostyle is prominent; the anterior crescent is smaller than the posterior crescent.

In the M1 with a wear stage III the anterior crescent is smaller than the posterior one and the mesostyle is still present. The M2 with this wear stage have moderately worn fossettes, the paracone and metacone are acute, the mesostyle and parastyle are prominent while the metastyle is poorly developed and there is a little developed anterior rib. The M3 have little worn and deep fossettes, the paracone and metacone are acute, the paracone and metacone are acute, the styles are moderately developed; there is a moderately developed anterior rib.

In wear stage IV, the P3 has a half moon outline, lack the fossette, the parastyle is well developed and the metastyle is strongly developed; between them there is a rib. The P4 also has a half moon shape, it lacks the fossette; the parastyle is slightly developed, the metastyle is well developed; between the style there is a moderately developed rib (Figures 3.1–3.4).

The M1 in wear stage IV does not have fossettes; the parastyle and metastyle are absent, the mesostyle is prominent and the occlusal surface is acute with the mesostyle as

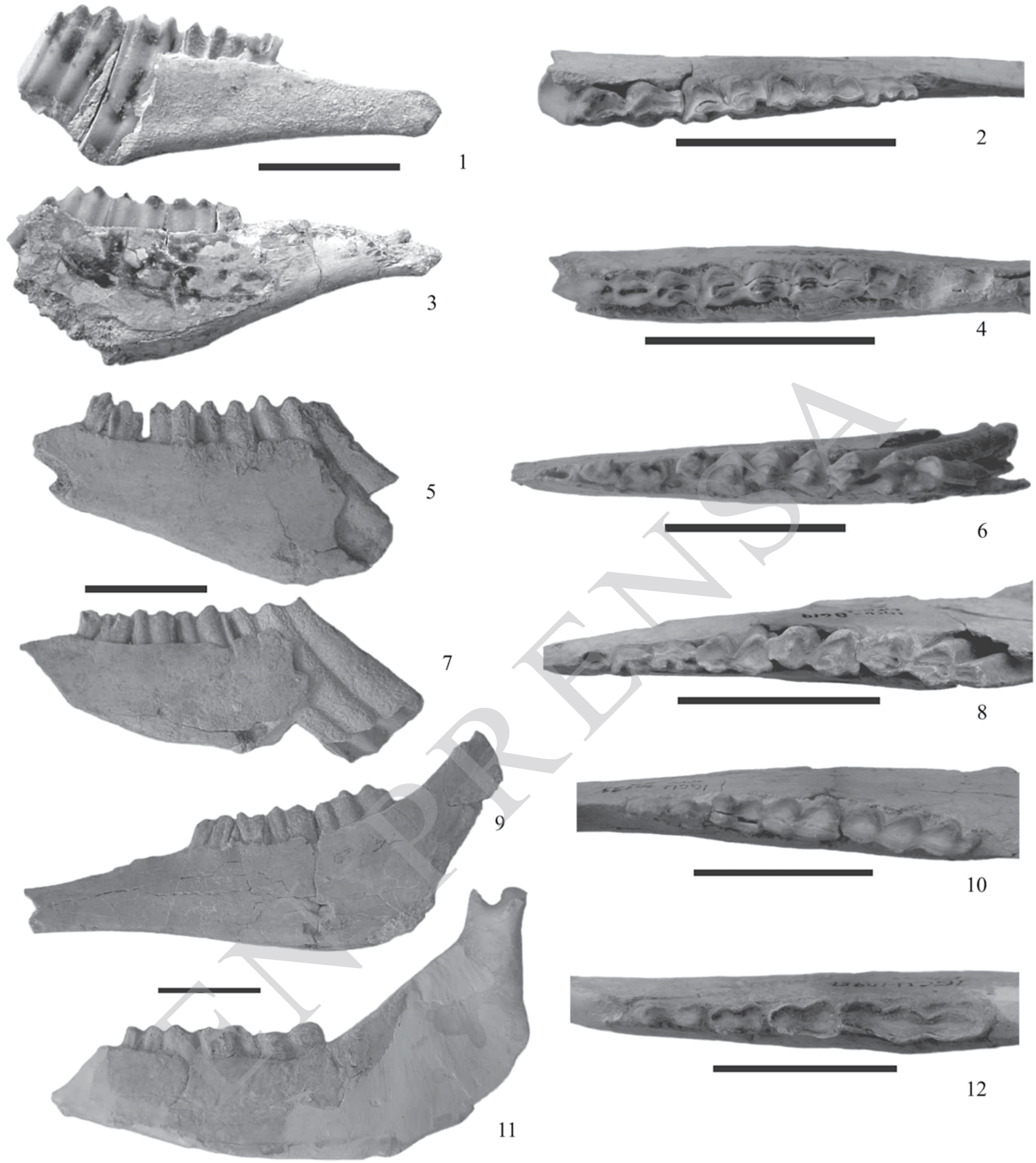




Figure 2. Mandibles and lower dentition of *Hexobelomeryx fricki* showing the tooth stage of wear displayed by the San Miguel de Allende specimens. IGM 9409, left mandible fragment with dp3-m3 in tooth wear stage I, 1. Lingual view, 2. Occlusal view. IGM 9383, left mandible fragment with partial p4-m3 in tooth wear stage II, 3. Lingual view, 4. Occlusal view. IGM 9433, right mandible fragment with p3-m3 in tooth wear stage III, 5. Lingual view, 6. Occlusal view. IGM 9376, right mandible fragment with p3-m3 in tooth wear stage IV, 7. Lingual view, 8. Occlusal view. IGM 9434, right mandible fragment with p3-m3 in tooth wear stage V. 9. Lingual view, 10. Occlusal view. IGM 9427, right mandible fragment with very worn p3-m3 in tooth wear stage V. 11. Lingual view, 12. Occlusal view. Scale bars equal 30 mm.

the higher structure. The anterior crescent of M1 is smaller than the posterior one. The anterior fossette of M2 in wear stage IV is heavily worn or absent and the posterior one is heavily worn, the parastyle is moderately or slightly developed, the mesostyle is prominent, the metastyle is moderately or slightly developed and the little developed anterior rib still is present. The fossettes of the M3 are moderately worn, the paracone and metacone are fairly

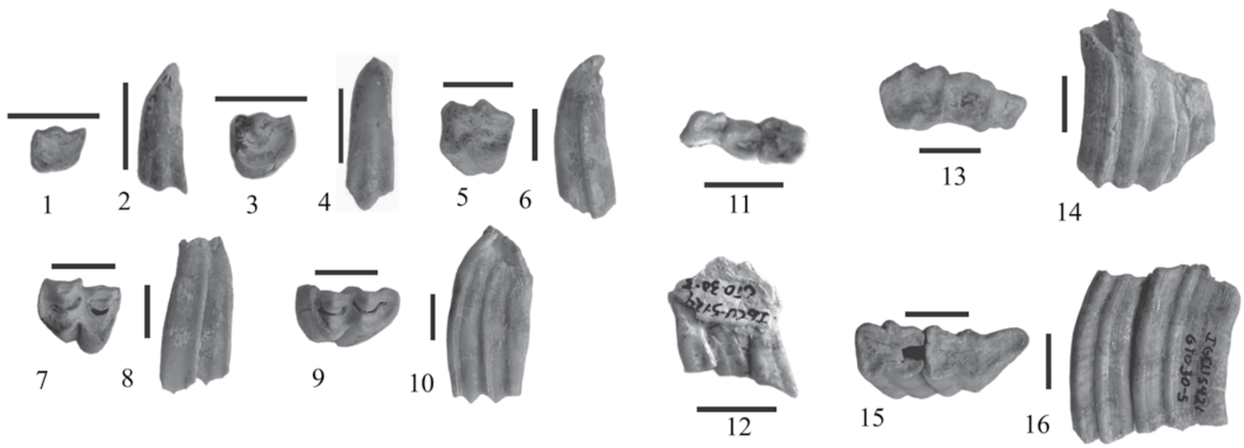


Figure 3. Upper dentition of *Hexobelomeryx fricki* from San Miguel de Allende, Guanajuato. IGM 9429-1, left P3 in stage of wear IV, 1. Occlusal view, 2. Labial view. IGM 9429-2, left P4 in stage of wear IV, 3. Occlusal view, 4. Labial view. IGM 9430, left M1 in stage of wear IV, 5. Occlusal view, 6. Labial view. IGM 9413, rigth M2 in stage of wear IV, 7. Occlusal view, 8. Labial view. IGM 9405, left M3 in stage of wear IV, 9. Occlusal view, 10. Labial view. IGM 9385-3, left P2-P4 in stage of wear V, 11. Occlusal view, 12. Labial view. IGM 9385-6, P4-M2 in stage of wear V, 13. Occlusal view, 14. Labial view. IGM 9385-5 and IGM 9385-4 left M2 and M3 in stage of wear V, 15. Occlusal view, 16. Labial view. Scale bars equal 10 mm.

acute, the parastyle is prominent while the mesostyle and metastyle are moderately developed; the anterior rib is little developed (Figures 3.5–3.10).

Finally, in wear stage V, the P2 has an ovoid outline (L= 4.7 mm, W= 4.0 mm), the P3 has a moderately developed mesostyle and rib; its parastyle is absent. The P4 lacks the style and rib. With additional wear the P3 and P4 show a triangular-to-ovoid outline. In the M1 and M2 the mesostyle persists but the other styles are absent, the anterior and posterior crescents tend to fuse. The M3 lost the fossettes, the metastyle is wider compared with previous stages of wear, forming a well developed heel that tends to fuse with the posterior crescent with additional wear (Figures 3.11–3.16).

**Material examined**. Locality 3009 arroyo La Carreta: IGM 9363, right M2; IGM 9364, right p4; IGM 9365, right M1; IGM 9366 and IGM 9367, left M2; IGM 9368 right M2; IGM 9369, right m2; IGM 9370, left m3; IGM 9371, M2; IGM 9372, left M2; IGM 9373, right m2; IGM 9374, left m2; IGM 9375, left M1. Locality 3074 Arrastracaballos: IGM 9376, right mandible fragment with p3-m3 and the p2 alveolus; IGM 9377, right m3; IGM 9378 and IGM 9379 left M3. Locality 3521 Coecillos: IGM 9380 right M1; IGM 9381, left M3; IGM 9382-1, right mandible fragment with p3, dp4 and m1 and IGM 9382-2, left mandible fragment with p3, dp4, m1 and erupting m2 of one individual; IGM 9383, left mandible fragment with the posterior part of p4-m3 (erupting); IGM 9384, left mandible fragment with m1-m3; IGM 9385-1, left mandible fragment with m2-m3, IGM 9385-2, right mandible with i3, c-m3; IGM 9385-3, P2-P4 series; IGM 9385-4, left M2 and IGM 9385-5, left M3; IGM 9385-6, right series with P4-M2; IGM 9385-7, right M3, all from a single individual; IGM 9386, right mandible with p4-m3 and the alveoli for p2 and p3; IGM 9387, IGM 9388, IGM 9389, IGM 9390, left m1; IGM 9391, right m2; IGM 9392, IGM 9393, left m2; IGM 9394, IGM 9395, IGM 9396, left m3; IGM 9397, IGM 9398, right m3; IGM 9399, right M1; IGM 9400, left M1; IGM 9401, left P4; IGM 9402, left M1; IGM 9403 and IGM 9404 left M2; IGM 9405, IGM 9406, IGM 9407, left M3; IGM 9408, right m3; IGM 9409, left mandible fragment with dp3-m2 (erupting). Locality 3487 Ferrocarril 2: IGM 9410 left m2; IGM 9411, left m3; IGM 9412, left M1; IGM 9413, right M2; IGM 9414 left M2. Locality 3510 Perros Bravos: IGM 9415, right p4; IGM 9416, left P3 and IGM 9417 left P4. Locality 3544 rancho San Martín: IGM 9418, right mandible fragment with p3-m2; IGM 9419, right M3. Locality 3403 La Rinconada**:** IGM 9420, right m2; IGM 9421, left M1; IGM 9422, right M1; IGM 9423, right M2; IGM 9424 and IGM 9425, left M2. Locality 3545 La Presa: IGM 9426, left m3. Locality 3524 Porkchop: IGM 9427, right mandible fragment with p3-m3. Locality 3546 Cara Cara: IGM 9428, left m2; IGM 9429-1, left P3 and IGM 9429-2, left P4 (both of a single individual); IGM 9430, left M1; IGM 9431, right

Table 2. Measurements of lower teeth of *Hexobelomeryx fricki* from San Miguel de Allende, Guanajuato, central Mexico.

| Tooth | Measurement | n | OR | $\bar{X}$ |
|---|---|---|---|---|
| p3 | L | 6 | 5.0–6.3 | 5.72 |
| | W | 6 | 2.8–3.9 | 3.1 |
| p4 | L | 10 | 5.6–8.3 | 6.92 |
| | W | 10 | 3.0–5.6 | 3.97 |
| m1 | L | 16 | 8.1–11.7 | 10.13 |
| | W | 16 | 4.8–6.6 | 5.72 |
| m2 | L | 25 | 10–14.5 | 12.26 |
| | W | 25 | 3.7–7.7 | 6.51 |
| m3 | L | 23 | 13.7–23.8 | 20.4 |
| | W | 23 | 4.3–7.3 | 6.54 |

Table 3. Measurements of mandibles of *Hexobelomeryx fricki* from San Miguel de Allende, Guanajuato, central Mexico.

| | Length alveolus p2–m3 | Length p3–m3 | Length m1–m3 | Depth of mandible below m3 |
|---|---|---|---|---|
| n | 4 | 5 | 9 | 8 |
| OR | 52.8–63.8 | 51.3–56.0 | 31.6–44.2 | 30.3–37 |
| $\bar{X}$ | 58.2 | 54.7 | 40.48 | 34.91 |

Table 4. Measurements of upper teeth of *Hexobelomeryx fricki* from San Miguel de Allende, Guanajuato, central Mexico.

| Tooth | Measurement | n | OR | $\bar{X}$ |
|---|---|---|---|---|
| P3 | L | 3 | 5.0-5.4 | 5.15 |
| | W | 3 | 4.5-5.0 | 4.67 |
| P4 | L | 4 | 6.4-7.9 | 6.86 |
| | W | 4 | 6.0-6.9 | 6.28 |
| M1 | L | 12 | 7.1-13.0 | 10.0 |
| | W | 12 | 7.6-9.4 | 8.7 |
| M2 | L | 15 | 10.9-16 | 13.76 |
| | W | 15 | 9.2-11.0 | 10.26 |
| M3 | L | 9 | 15.0-18.4 | 16.68 |
| | W | 9 | 8.3-9.9 | 9.12 |

M1; IGM 9432, left M2. Locality 3556 Earthwatch: IGM 9433, right mandible fragment with p3-m3 and the alveolus for p2. Locality 3564 arroyo Tepalcates: IGM 9434, right mandible with p3-m2 and the alveolus for p2; IGM 9435, left m2. Locality 3566 Candado: IGM 9436, left mandible fragment with m1-m3.

**Distribution**. Latest Hemphillian (Hh4) of Chihuahua (Furlong, 1941; Lindsay *et al.*, 2006); late early Hemphillian to latest Hemphillian (Hh2 to Hh4), Blancan I and Blancan III of San Miguel de Allende, Guanajuato.

**Discussion**. The studied specimens from the Hemphillian and Blancan of San Miguel de Allende show a close morphology and dimensions when compared to the fossil material of *Hexobelomeryx fricki* from the Yepómera/Rincón fauna.

When comparing the mandible fragment IGM 9433 and the isolated lower molars IGM 9410, IGM 9411 and IGM 9373, all in wear stage III with CIT 2787 (paratype), a mandible fragment with p3-m3, also in wear stage III, it is evident that they share a sharp diastemal crest and a very deep mandible below m2 and m3; they have very hypsodont teeth; the p3 shares a wide, anterior valley. They also share a p4 with a well developed paraconid; they show a short p3 and p4 compared to the molars; the parastylid and entostylid of the m1 are little developed; the parastylid and entostylid of the m2 are moderately developed, and the m3 have a well developed parastylid and acute metaconid and entoconid.

The mandible fragments with teeth and isolated lower molars in wear stage I and II of Guanajuato, have moderately to well developed stylids, as are those with slight wear m2 and m3 molars of CIT 2787.

The specimen CIT 2793, a mandible fragment with a tooth wear stage V and the San Miguel de Allende specimens IGM 9384, IGM 9386 IGM 9434 and IGM 9436, share a triangular outline of premolars without any trace of fossettids, a lack of stylids in the molars, a flat lingual wall on m1, a slightly developed entostylid in m2, and m3 with rounded worn entostylid; the mandibles from Chihuahua and Guanajuato are also deep below m2 and m3. The isolated lower molars in wear stage V also show a similar degree of stylids development to those of teeth seen in CIT 2793.

The mandible fragments IGM 9427, IGM 9385-2 and CIT 2799 (paratype) are more worn than CIT 2793 or IGM 9434, they show a rather ovoid outline of the molars because of the fusion of anterior and posterior crescents, they share the absence of molar stylids and a fusion of the m3 entostylid with the second crescent. Also, in the specimens from Guanajuato and Chihuahua the mandible is deep and the diastemal crest is sharp.

Regarding the upper dentition, the premolars from San Miguel de Allende in wear stage IV have a better developed metastyle and rib than those of CIT 2781 (paratype), a maxillary fragment with P3-M3 in wear stage V; but in IGM 9385-3, a premolar series in wear stage V, the styles have disappeared and the premolars have an ovoid outline, as is observed in CIT 2781.

The M1 and M2 from San Miguel de Allende in wear stage V and the Chihuahua specimen lack fossettes, have a mesostyle but they lack the other two styles; the anterior crescent of these molars is smaller than the posterior one, especially in the M1. The M3 in wear stages IV and V share with the Yepómera specimen a well developed parastyle and a moderately developed mesostyle; also in the M3 with V wear stage the metastyle forms a well developed heel that fuses with the second crescent, as seen in the M3 of CIT 2781.

Additionally, the depth of the studied mandibles below the m3 is within the observed range (30-37 mm) in *Hexobelomeryx fricki* (Table 3) as is the diastema length (42-51 mm) (Furlong, 1941). Also, the teeth dimensions are within the range reported for the species (Table 2 and 4), as is the p3-p4 mean length percent (26% to 30%) regarding the m1-m3 mean length (Tables 2 and 3).

In his description of *Hexoblomeryx fricki*, Furlong (1941) mentions various features that are present in the San Miguel de Allende specimens, such as a well developed masseteric ridge in rami, a short diastema, hypsodont teeth, short upper teeth series, an absence of metastylid in lower molars, an entostylid that forms a talonid in well worn m3's, small upper premolars when compared to upper molars, a persistent mesostyle on upper molars and a well developed heel that is formed by the metastyle in well worn M3's.

All of the above mentioned characters, as well as the close dimensions observed between the Guanajuato specimens and those of Chihuahua, allow the confident classification of specimens from San Miguel de Allende, Guanajuato, as *Hexobelomeryx fricki*.

In their diagnosis of *Hexobelomeryx fricki,* Janis and Manning (1998) mention the absence of a middle rib in the P4; nevertheless, in the San Miguel de Allende specimens this rib is present in the premolars with a wear stage IV, disappearing in a wear stage V. So, the presence or absence of the middle rib depends on the P4 wear stage.

After comparing the San Miguel de Allende specimens with UCMP 3978, a left mandible of *Tetrameryx* with p2-m3, the morphological differences are evident, since the mandible from California is shallow, its diastema is long, their premolars are large when compared with the molars, its p2 is almost as large as p3, and the worn p4 is bilobated with a well developed anterior fossettid.

The studied specimens differ from the Hemphillian *Texoceros* in their larger teeth dimensions, higher hypsodonty, larger p3-p4 mean length percent when compared with the mean m1-m3 length, and shallower mandibles (Hesse, 1935); they also differ from the Hemphillian *Subantilocapra* and the Blancan *Capromeryx* in their much larger teeth dimensions, hypsodonty and the less developed styles (Webb, 1973; Morgan and Morgan, 1995; Jiménez-Hidalgo *et al.*, 2004).

## PALEOBIOLOGICAL CONSIDERATIONS

### Age at death distribution in the *Hexobelomeryx fricki* sample

We estimated the probable absolute age of *Hexobelomeryx fricki* from San Miguel de Allende, at the the time of their death, in order to obtain an approximation of their mortality profile. We used the wear-scoring system proposed by Lubinski (2001) for *Antilocapra americana*.

The pronghorn antelope *A. americana* is the only surviving species of the Family Antilocapridae, so we consider it as a good proxy of the life history of *H. fricki* since it is its closest living relative.

The lower cheek teeth represent 51.8 % of the entire sample. Since the upper teeth show the same stage of wear-pattern distribution (with few specimens with a stage of wear II-IV and a great majority with a stage of wear V), we considered that the mortality profile displayed by the lower teeth, adequately reflects that of the entire sample.

Table 5 and Figure 4 show that less than 10 % of individuals are younger than one year, fewer are around one year; less than 15 % are around 3.3-4.3 years and the best-represented age class is that of more than nine years, representing more than 60 % of the sample. This pattern of several young individuals and a large majority of old individuals is also observed if we divide the sample in a Hemphillian set and a Blancan set, so for the sake of simplicity we treated them together.

Two kinds of idealized mortality profiles characterize mammalian populations: catastrophic and attritional. In the catastrophic profile the young individuals are the most abundant and the successive age groups contain progressively fewer individuals, whereas in the attritional profile the very young and old individuals are the best represented, while prime-age adults are rare (Klein, 1982; Steele, 2003).

Table 5. Probable absolute age at death of the *Hexobelomeryx fricki* individuals from the Pliocene of San Miguel de Allende, Guanajuato, central Mexico.

| Pad (yrs) | tooth wear stage | % individuals |
|---|---|---|
| 0.7-0.8 | I | 9.3 |
| 1.3-1.4 | II | 2.32 |
| 3.3 | III | 9.3 |
| 3.5-4.3 | IV | 11.62 |
| > 9 | V | 65.1 |

The San Miguel de Allende mortality profile of *H. fricki* shows a "J" shape, somewhat similar to the idealized attritional profile, but with an impoverishment of very young individuals and a much higher proportion of old individuals (Figure 5).

This underrepresentation of very young individuals in the studied sample can be explained taking into account that juvenile bones and deciduous teeth are more susceptible to carnivore ravaging, compaction, fragmentation and soil leaching than adult specimens (Steele, 2003, 2004), so, they have a higher probability of being destroyed than those of adult specimens.

On the other hand, the overrepresentation of old individuals (> 9 years) in the sample when compared with the idealized attritional mortality model, suggests that the individuals of *H. fricki* from Guanajuato would have had

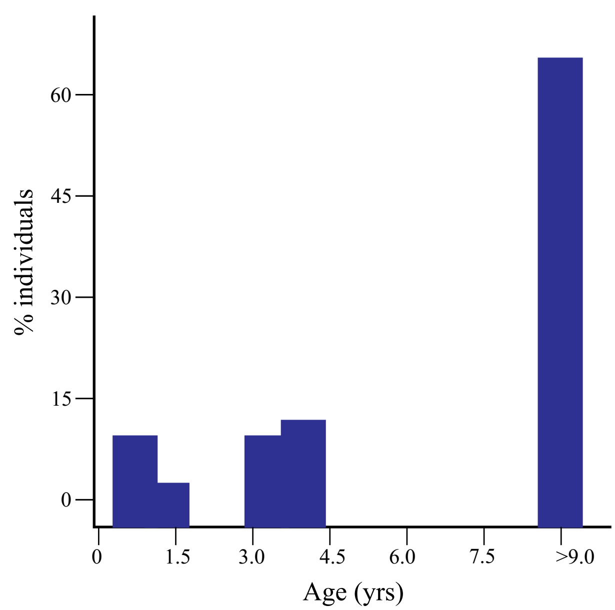


Figure 4. Distribution of probable age at death of the *Hexobelomeryx fricki* sample from San Miguel de Allende, Guanajuato, central Mexico.


Figure 5. Geographic distribution in North America of *Hexobelomeryx* during the Hemphillian land mammal age. 1. Yepómera and Matachic localities of Chihuahua, 2. Tecolotlán locality, state of Jalisco, 3. San Miguel de Allende, state of Guanajuato, 4. Zietla-Tehuichila locality, state of Hidalgo. **?** denotes the possible record of this genus in USA.

a great expectancy of life after surviving the first years (there are not individuals represented in the 4.5-7.5 years rank) (Figure 5), taking into account that the life span of *A. americana* reaches more than nine years (Howard, 1995). When the individuals become very old, probably they naturally died or maybe predators hunted them, given that they become more vulnerable; afterwards they were incorporated in the fossil record.

### Body mass of *Hexobelomeryx fricki* from Guanajuato

We estimated the probable body mass of several specimens within each stage of tooth wear to have an approximation to body mass between the different ages at death represented in the sample.

The estimated values in Table 6 do not show any tendency towards the increment or diminution of body mass as tooth wear stage advanced. This suggests that since early in the ontogeny, the teeth dimensions of *Hexobelomeryx* reflect the body mass of adults. So, to recover the body mass of juveniles and young adults it will be necessary to use cranial and mandible data, which reflect the change in dimensions during the ontogeny, but at present, such variables are unavailable in the San Miguel de Allende sample.

The lowest body mass values are from tooth stage of wear II and not tooth stage of wear I (Table 6). In tooth wear stages III to V there is some overlap between the ranges of the estimated body masses. The values derived from the LMRL equation show the widest range (around 6 kg).

The lowest body mass values observed in tooth stage of wear V for the LMRL and SLMA equations (12.73 kg and 13.57 kg), could result from the small dimensions of the very heavy-worn molars of some specimens. Given that both equations are univariate, the influence of these teeth values is higher than in the multivariate algorithms of Mendoza *et al.* (2006), where some of these teeth values can be buffered with the other variables, diminishing the observed body mass value range (Table 6).

On the other hand, some values are similar in different tooth-wear stages (Table 6) and consistently, the higher body mass estimations were obtained from the body mass determination algorithms of Mendoza *et al.* (2006).

If as in *Antilocapra americana*, *Hexobelomeryx fricki* reaches its adulthood between 1.5- 2.0 years (Howard, 1995), the body mass of adults in the San Miguel sample was reached in tooth wear stage II or III (Table 6). For comparison, the body mass of *Antilocapra americana* in Texas has a mean of 40-41 kg and of 50 kg in Alberta, varying seasonally from 47 to 70 kg (O'Gara, 1978).

### Geographic distribution and biochronology

*Hexobelomeryx* seems to be an endemic mexican pronghorn (Figure 5), with records in the late early Hemphillian of Hidalgo and the late Hemphillian of Jalisco, as well as the latest Hemphillian of Chihuahua (Carranza-Castañeda, 1994; Montellano-Ballesteros, 1997; Carranza-Castañeda and Miller, 2000; Miller and Carranza-Castañeda, 2001, 2002). In San Miguel de Allende, *Hexobelomeryx fricki* is present from the late early Hemphillian (Hh2) to Blancan III, from 7.0 to 3.0 Ma (Table 1). Its record in the late early Hemphillian and the Blancan III of Guanajuato is the oldest one and the youngest ocurrence in North America.

There are two doubtful late and latest Hemphillian records of the genus in Texas and Nevada, southwestern North America, that if confirmed as *Hexobelomeryx* would extend its geographic range towards the north (Figure 5).

After the latest Hemphillian extinction event, *H.*

Table 6. Estimated body mass of *Hexobelomeryx fricki* from the Pliocene of San Miguel de Allende, Guanajuato, central Mexico. In this tooth stage of wear the body values were obtained from one individual. *Value obtained with equation for FLML of Janis (1990)

| Tooth wear stage | Janis (1990) | | Mendoza *et al.* (2006) | |
|---|---|---|---|---|
| | LMRL | SLMA | Algorithm 7.2 | Algorithm 7.3 |
| I | 19.27* | 16.09 | -- | -- |
| II+ | 10 | 10.75 | 14.89 | 30.1 |
| III | 18.8 | 18.0–18.45 | 25.41 | 29.42 |
| IV | 18.13 | 15.3–18.49 | 25.51 | 29.6 |
| V | 12.73-19.29 | 13.57–17.1 | 24.3-27.64 | 26.8-29.51 |

*fricki* only survived during the Blancan land mammal age in central Mexico, in the San Miguel de Allende area. Janis and Manning (1998) and Davis (2007) wrongly record *H. fricki* from the Blancan of Chihuahua, because the Matachic locality is of Hemphillian age (Lindsay *et al.*, 2006).

## CONCLUSIONS

The presence of *Hexobelomeryx fricki* in the San Miguel de Allende graben is established based upon description and comparison of teeth and mandible specimens with the paratypes of this pronghorn species from the Yepómera/Rincón fauna of Chihuahua.

The mortality profile of the *H. fricki* tooth sample from the study area is an attritional one, with few juveniles and a large majority of old individuals.

The body mass estimations based on the San Miguel de Allende specimens indicate that the *H. fricki* individuals had a body mass that ranged from 10 to 30 kg according to their age at death.

*Hexobelomeryx fricki* was present in the San Miguel de Allende graben, state of Guanajuato since the late early Hemphillian to the Blancan III. Its record in Guanajuato extends the geographic distribution of the species from northwestern Mexico to central Mexico during the Late Hemphillian.

The presence of *H. fricki* in late early Hemphillian age sediments and in the Blancan age deposits of San Miguel de Allende represents its oldest and youngest occurrence in North America, respectively.

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