A LATE MIOCENE DOLICHOTINAE (MAMMALIA, RODENTIA, CAVIIDAE) FROM URUGUAY, WITH COMMENTS ABOUT THE RELATIONSHIPS OF SOME RELATED FOSSIL SPECIES

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ABSTRACT. The oldest dolichotine from Uruguay (late Miocene deposits of southwestern) is described and here assigned to the genus “Prodolichotis” Kraglievich, 1932. It is intermediate in size between Pediolagus salinicola (Burmeister, 1876) and Dolichotis patagonum (Zimmermann, 1780) and similar to “Prodolichotis” lacunosa (Ameghino, 1888). The material consists in an incomplete skull which has a diastema longer than P4-M3 length, the nasolacrimal foramen absent in lateral view, the anterior border of mesopterygoid fossa positioned between the anterior and posterior prisms of M2 and the internal posterior fold of M3 has diverging borders forming an angle less than 90º. This M3 morphology shared with the Dolichotinae-Caviinae clade suggests that parallel borders are a derived feature in some Dolichotinae and the condition observed in the Caviinae is a primitive state. Judging by the morphological pattern presented by “Prodolichotis” pridiana Fields (1957)—nasolacrimal foramen in the maxilla, interorbital width less than the braincase width, and diverging M3 fold—we agree with previous opinions that this species should be included in the Caviinae instead of Dolichotinae. It is discussed a close relationship between Orthomyctera Ameghino, 1889 and Caviinae judging by their similar morphological pattern including interorbital width less than the braincase width, molar series with similar length or longer than the diastema length, nasolacrimal foramen exposed laterally in the maxilla, and similar configuration of the M3 and skull size and overall shape. The occurrence of a dolichotine in the late Miocene of southwestern Uruguay suggests open and probably arid or semiarid terrestrial environments.

RESUMEN. Un Dolichotinae (Mammalia, Rodentia, Caviidae) del Mioceno tardío de Uruguay, con comentario sobre las afinidades de especies fósiles relacionadas. Se describe el registro más antiguo de Dolichotinae para el Uruguay proveniente de depósitos del sur-oeste y asignables al Mioceno tardío y se incluye dentro del género “Prodolichotis”. Su tamaño es intermedio entre las especies Pediolagus salinicola y Dolichotis patagonum y similar a “Prodolichotis” lacunosa. El material consiste en un cráneo incompleto con el diastema más largo que la serie P4-M3; foramen nasolacrimal no apreciable en vista lateral; borde anterior de la fosa mesopterigoidea ubicado entre los prisms del M2; hendidura posterior interna del M3 con bordes divergentes formando un ángulo menor de 90º. Esta configuración del M3 compartida por el clado Dolichotinae-Caviinae sugiere que la condición de poseer bordes paralelos en este molar que presentan los actuales Dolichotinae podría ser una característica derivada y no primitiva, y la configuración existente en el M3 de los cavinos primitivo. Teniendo en cuenta algunas características morfológicas de “Prodolichotis” pridiana —foramen nasolacrimal visible en vista lateral, ancho interorbitario menor que el ancho de la caja craneana, hendidura posterior interna del M3 con bordes divergentes— concordamos con opiniones previas, en que esta especie debe incluirse en Caviinae y no en Dolichotinae. Se discuten evidencias para incluir al género Orthomyctera dentro de la subfamilia Caviinae: ancho interorbitario marcadamente menor que el de la caja craneana;
INTRODUCTION

Despite the fact that there are different opinions about the monophyletic status of dolichotines as a subfamily of Caviidae (Quintana, 1997, 1998), they are recognised as peculiar hystricognath rodents whose age ranges from the late Tertiary to Recent (Vucetich and Verzi, 1995). Living Dolichotinae are endemic to southern South America (Redford and Eisenberg, 1992) and the two living species are usually arranged in one genus Dolichotis or in two different genera, Dolichotis and Pediolagus, the “mara” and “conejo del palo” respectively (see Kraglievich, 1930; Mares and Ojeda, 1982; Wilson and Reeder, 1993; Quintana, 1998).

Dolichotis patagonum is widespread in central and southern Argentina and Pediolagus salinicola is distributed in NW Argentina and the Chaco of Paraguay and southern Bolivia (Wilson and Reeder, 1993) (Fig. 1). These species inhabit arid areas, especially desert, grassland scrub, thorn scrub and dry forest (Mares and Ojeda, 1982).

There is also a controversy among authors about the identity and the subfamilial relationships of several fossil taxa described as dolichotines or caviines (Quintana, 1997, 1998). As a complete taxonomic revision of the entire subfamily including the fossil taxa is beyond the scope of this paper some taxa are included in quotation-marks.

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Fossil dolichotines are known from several localities in the Neogene and Quaternary ages in South America, but in general the record is scarce and not well studied. The oldest record of the group comes from the Miocene of Colombia and Argentina, whereas the Pliocene record is restricted to Argentina (Fields, 1957; Walton, 1997; Cione et al., 2000) (Fig. 1). Calcaterra (1972) referred Dolichotis major (Gervais and Ameghino, 1880) to Pleistocene sediments of southwestern Uruguay, the only fossil dolichotine known from this country.

In this paper we describe the oldest record of the subfamily Dolichotinae from Uruguay (Arazatí, San José Department; the Camacho Formation) and discuss the taxonomic value of dental and cranial characters in order to improve our knowledge of this poorly known group. Comments about the taxonomic assignment of the fossil species “Prodolichotis” pridiana and fossil genus Orthomyctera to the subfamily Caviinae are also provided.

MATERIAL AND METHODS


The following cranial material was used for comparison:

Dolichotis patagonum: MACN-Ma: 302; 303; 304; 917; 29879; 26209; 35406; 49132; 27152; 14532; 28183; 15533; 29894; 13755; 2665; 28190; 4319; 29193; 15534; 2516; 13756; 4959. IAVA: 1 specimen: w/n. MLP-DZV: 488, 226, 208, 597, 247, 251, 30.X.95.11, 371, 1699, 687, 1783, 2.VI.60.11, 418, 230, 723, 369, 638.

Pediolagus salinicola: MACN-Ma: 41218, 29872, 41216; 28188; 4326; 17363; 28143; 30239; 28144; 30154; 33166; 30390; 41217; 3228; 26210; 4279; 30155. MLP-DZV: 672, 673, 1081, 2671. Orthomyctera rigens (Ameghino, 1889): MACN-Pv: 7319, 1661-62. Orthomyctera andina (Rovereto, 1914): MACN-
A LATE MIOCENE DOLICHOTINAE FROM URUGUAY

Fig. 1. A) Geographic occurrences of Miocene and Pliocene Dolichotinae in South America: 1) Middle Miocene of Colombia, Villavieja Fm. (innominated genus following Walton, 1997), 2) Late Miocene, Catamarca, Argentina, Andalhuala Fm., 3) Late Miocene Entre Ríos, Argentina, Ituzaingó, Fm. 4) Pliocene, Buenos Aires Province. Montehermoso Fm., 5) Pliocene, Chapadmalal, Buenos Aires Province, Argentina. Dotted and shaded areas: recent distribution of Dolichotinae. B-C) geographic locality of MNHN-1633 Dolichotinae fossil from Uruguay. The arrow shows the fossil location.


Six cranial and dental linear dimensions were measured with a caliper to the nearest 0.1 mm. In Table 1 we provide character abbreviations. Values in Table 2 were calculated by means of Statistic 4.2-1993 software. Occlusal surfaces of upper molars were drawn with a Zeiss Stemi SV11 drawing tube mounted on a stereomicroscope.

GEOLOGICAL SETTING AND BIOSTRATIGRAPHY

Three lithostratigraphic units can be recognised in Arazatí outcrops, these are from the base to the top: Camacho, Raigón (= San José Formation) and Libertad formations (Fig. 2). The outcrops of the Camacho Formation at this locality (considered the Kiyú Formation by Francis and Mones, 1965) are the upper facies of a Late Miocene transgressive episode, which includes ostreid biostromes, “patch reefs” and ichnofossils in a greenish-gray clayey silt (Martínez, 1994; Sprechmann et al., 2000; Verde, 2002). The fossil mammal assemblage
Table 1

Measurements (mm) of the Arazatí material (MNHN-1633) and comparative specimens included in the genus *Dolichotis* (D), *Orthomycterria* (O) and “*Prodolichotis*” (P). 1: constriction interorbital maximum, 2: palatal width (including M³), 3: diastema length, 4: P⁴-M³ length, 5: M³ length, 6: M³ width.

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Table 2

Statistical values for living species *Dolichotis patagonum* and *Pediolagus salinicola*. n: sample size; x: mean; min. and max.: range; ds: standard deviation. Measurements explained in Table 1.

<table>
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of the Camacho Formation at Arazatí cliffs is represented by terrestrial taxa of Huayquerian-“Mesopotamian” affinities (Perea et al., 1994). It is important to note that Cione et al. (2000) consider the “Mesopotamian” as an invalid unit correlating the “conglomerado osífero” of the Ituzaingó Formation (“Mesopotamian”) with the Late Miocene Huayquerian stage. They referred *Prodolichotis* to the Late Miocene Ituzaingó Formation from Paraná of Argentina.

Transport processes explain the occurrence of terrestrial mammals along with estuarine and marine ostreids and ray teeth remains, freshwater turtles and flamingoes (Perea et al., 1996; Ubilla et al., 1990). The Dolichotinae remain was found a few centimeters above the ostreid biostromes and close to a tooth ray. The taphonomic and sedimentological features of this particular lithofacies of the Camacho Formation suggest an estuarine or marginal shallow-water marine depositional environment
Fig. 2. Stratigraphic profile of Arazatí exposures. The arrow indicates the location of "Prodolichotis" sp. c: clay, s: sand, f: fine, m: medium, c: coarse, p: pebbles. Colour codes following Rock Color Chart Committee. 1980. Geological Society of America.
(Perea et al., 1996), similar to that described by Behrensmeyer and Hook (1992).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758  
Order RODENTIA Bowdich, 1821  
Suborder HYSTRICOGNATHI Tullberg, 1899  
Superfamily CAVIOIDEA Kraglievich, 1930.  
Family CAVIIDAE Waterhouse, 1839  
Subfamily DOLICHOTINAE Pocock, 1922  

Genus “Prodolichotis” Kraglievich, 1932  
“Prodolichotis” sp. (Figs. 3 and 4)

Material referred — MNHN-1633: fragmented skull with incisors, diastema, palate with left and right P4-M3, part of the infraorbital foramen and incomplete zygomatic arches.  
Horizon and locality — in silty sandy and grayish-green sediments of the Camacho Formation (=Kiyú Lithofacies), immediately above an oyster bank (Fig. 2). About 6 km southeast of Sauce Creek, Departament of San José, Puerto Arazatí, Uruguay (Fig. 1).

Description — incomplete skull of a Dolichotinae with some linear dimensions modified by lateral deformation; intermediate in size between Pediolagus salinicola and Dolichotis patagonum and similar to that of “Prodolichotis” lacunosa. Incisors broken at the alveolar margin; diastema longer than P4-M3 length; nasals wide and fragmented; in lateral view the nasolacrimal foramen is absent; P4-M2 sub equal with cordiform prisms connected by an isthmus and covered with an interrupted layer of enamel; internal fold with cementum; external folds delimited by the anterior and posterior prisms; M3 with suboval additional posterior prism, smaller than the others; the internal fold between the second and third prisms slightly penetrating and without cementum delineated by diverging borders at an angle less than 90°; unexcavated and short palate with posteriorly diverging tooth rows; anterior border of mesopterygoid fossa positioned between the anterior and posterior prisms of M3.  
Measurements — see Table 1.

DISCUSSION AND CONCLUSION

Following the taxonomic revision of Quintana (1998) we consider the skull of Arazatí as a Dolichotinae on the basis of the following characters: the diastema is longer than P4-M3 length, the nasolacrimal foramen is absent in lateral view and the mesopterygoid fossa positioned at the level of the anterior and posterior prisms of M3. It is important to note that this character assemblage is shared by all taxa in the subfamily Dolichotinae.

With regard to the living species of Dolichotinae, the Arazatí material differs in size and in M3 structure. Its size is intermediate between Dolichotis patagonum and Pediolagus salinicola and similar to that “Prodolichotis” lacunosa (Figs. 4, 5 and Table 2). Despite the fact that upper tooth row morphology is quite similar in the examined genera (Fig. 4), M3 configuration allows one to differentiate three groups which laudably convey its variability: a) in Dolichotis and Pediolagus the second internal fold is penetrating and has cementum; the posterior border of the second prism and the anterior border of the additional posterior prism tend to be parallel, b) in Orthomyctera rigens and Orthomyctera andina (which are not considered as dolicotines by Quintana, 1998) there is approximately 90° between the borders of the internal folds of the second and third prisms, c) the “Prodolichotis” group and the Arazatí material show diverging borders with an angle tending to be less than 90°, an intermediate configuration between the two previous groups.

Kraglievich (1932) described the genus Prodolichotis and referred to it several species defined on the basis of skull and mandible material. Though the genus need revision, the fossil from Uruguay fit well within its morphological characteristics. Taking into account the similar size, shape and molar configuration, we assign MNHN-1633 to “Prodolichotis” sp. and we consider the available characters insufficiently diagnostic to describe a new species nor assign it to previously described species.

In the phylogenetic analysis provided by Quintana (1998), an M3 with diverging borders is considered a synapomorphy of Caviinae.
Nevertheless, in our point of view, this should be revised in light of the variability and intermediate condition observed in “Prodolichotis”. In fact, diverging borders may have been the ancestral state of the Dolichotinae-Caviinae clade, and the tendency to become parallels a derived feature in some Dolichotinae. So, at this level of resolution the condition observed in the Caviinae could be interpreted as a primitive state. However, the Caviinae Microcavia robusta Gervais and Ameghino, 1880 has a deep flexus with parallel borders (Quintana, 1996) which could suggest an independent evolution of this character in each subfamily.

The species “Prodolichotis” pridiana described by Fields (1957) from the Miocene of Colombia differs from the material from Uruguay by several characters such as the presence of the nasolacrimal foramen in the maxilla, interorbital width less than the braincase width, and clearly diverging M3 flexus. This set of characters is shared with the caviines. Nevertheless, diastema length is longer than...
cheek teeth length as in dolichotines. Judging by the morphological pattern presented by “Prodolichotis” pridiana, the generic and subfamilial relationships of this taxon need to be revised. We agree with Quintana (1998) that this species should be included in the Caviinae instead of the Dolichotinae. It is also interesting to note that this suite of characters is also found in the peculiar living caviine Kerodon Cuvier, 1825. In caviines $P_4$ has two prisms with an additional elongation in the anterior prism which in general does not become a true prism. In Kerodon and “Prodolichotis” pridiana this additional elongation becomes a well defined prism. This also suggests a relationship between these two taxa.

There is striking evidence in favour of the exclusion of Orthomyctera from the Dolichotinae as was suggested by Quintana (1998). Orthomyctera, was described by
Ameghino (1889) and was represented by four species in his original description. In a more restricted sense, considering those species defined on skull material (O. andina and O. rigens), this genus shows a similar morphological pattern to genera of Caviinae. Indeed, this genus has an interorbital width less than braincase width, molar series with length equal to or longer than diastema length, a well-developed nasolacrimal foramen, the third upper molar of similar configuration and similar skull size and overall shape. With reference to size, this genus is clearly smaller than the presumed members of Dolichotinae (Fig. 5).

“Orthomyctera” chapalmalense resemble Dolichotis patagonum in morphology and size (Fig. 5). “Orthomyctera” chapalmalense should not be included in this genus as was first suggested by Kraglievich (1930), and should instead be considered a dolichotine arguably Dolichotis. Indeed, “Orthomyctera” chapalmalense has a diastema longer than P4–M3 length, the mesopterygoid fossa positioned at the level of the anterior and posterior prisms of M2, the nasolacrimal foramen is not observed in lateral view, and the posterior border of the second prism and the anterior border of the additional posterior prism in M3 are parallel.

The continental late Miocene of Uruguay is not preserved in the landscape of this country. Consequently, the majority of vertebrates included in the paralic deposits of the Camacho Formation are our only window into the terrestrial and fluvial environments of this period. From the ecological requirements of its closest living relatives among the dolichotines, the record of “Prodolichotis” in the late Miocene of southwestern Uruguay suggests open and probably arid or semiarid terrestrial environments. Lagostomopsis Kraglievich, 1926, is also known from these sediments (Francis and Mones, 1965; Perea et al., 1994). Its most closely-related living genus, Lagostomus, inhabits grasslands and thorn scrubs. Even though the late Miocene dolichotines may have had different ecological requirements than the living species, these coincident species provide a likely environmental setting.

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