New genus of giant Dinomyidae (Rodentia: Hystricognathi: Caviomorpha) from the late Miocene of Uruguay

Author(s): Andrés Rinderknecht, Enrique Bostelmann T., and Martín Ubilla

Source: Journal of Mammalogy, 92(1):169-178. 2011.
Published By: American Society of Mammalogists
DOI: 10.1644/10-MAMM-A-099.1
URL: http://www.bioone.org/doi/full/10.1644/10-MAMM-A-099.1

Journal of Mammalogy, 92(1):169–178, 2011

New genus of giant Dinomyidae (Rodentia: Hystricognathi: Caviomorpha) from the late Miocene of Uruguay

Andrés Rinderknecht,* Enrique Bostelmann T., and Martín Ubilla

Museo Nacional de Historia Natural, CC 399, Montevideo, Uruguay (AR, EBT)
Departamento de Evolución de Cuencas, Facultad de Ciencias, Iguá 4225, CP 11400, Montevideo, Uruguay (MU)

* *Correspondent: rinderk@adinet.com.uy*

In this contribution we describe the fossil remains of a new genus and species of a giant rodent, *Arazamys castiglionii* (Mammalia, Rodentia, Dinomyidae), from Arazatí beach in San José Department, southern Uruguay. The specimen was exhumed from pelitic sediments of the Camacho Formation, biostratigraphically assigned to the late Miocene Huayquerian South American Land Mammal Age. The remains include an incomplete skull (braincase, auditory region, and nearly full dentition) and the atlas. Based on comparative studies of the anatomy of the auditory region, we describe 2 morphologies for the subfamily Eumegamyinae, 1 characterized by a short meatus acusticus externus, a great development of the foramen stylomastoideum, and a conspicuous ectotympanic cavity, and a 2nd characterized by a long meatus acusticus externus and lack of the ectotympanic fossa. The potential taxonomic and systematic value of the auditory region in Dinomyidae is discussed.

Key words: auditory region, Camacho Formation, Huayquerian South American Land Mammal Age, new Eumegamyinae, pacarana

DOI: 10.1644/10-MAMM-A-099.1

Dinomyidae (Peters, 1873) Alston, 1876, is 1 of the 3 families of giant rodents known from South America (Bondesio 1978). Currently, the family includes only the pacarana (*Dinomys branickii* Peters, 1873), a peculiar but poorly studied long-headed cursorial Amazonian caviomorph considered among the largest living rodents, with a body mass that approximates 15 kg (Collins and Eisenberg 1972; Peters 1873; Pocock 1926; Sanborn 1931; White and Alberico 1992). Contrary to this impoverished present record, the past diversity of the group was notable, with a large number of fossil genera and species reaching body sizes even larger than that of the pacarana. The most extreme is the giant *Josephoartigasia monesi*, the largest rodent ever recorded with an estimated mean body mass close to a ton (Rinderknecht and Blanco 2008; but see Blanco 2008; Millien 2008). The fossil record of the Dinomyidae undoubtedly begins during the middle Miocene (Friasian South American Land Mammal Age), but a genus (*Branisamys*) from the late Oligocene Salla beds in Bolivia (Deseadan South American Land Mammal Age) has been placed tentatively in the family by some authors (see discussion in Vucetich et al. 1999). Fossil members of the Dinomyidae have been described from almost every South American country (Fig. 1), with the collections from Argentina, Colombia, Venezuela, and Uruguay being the most important.

Although the 1st described fossils of the family date back to the late 19th century (Ameghino 1883a, 1883b, 1885, 1886, 1889, 1891a, 1891b; Burmeister 1885), the phylogeny of Dinomyidae never has been addressed using a modern cladistic approach. The revision by the Argentine paleontologist Lucas Kraglievich (1926, 1932a, 1932b) remains as the present systematic arrangement for the entire family. Following Kraglievich's main framework, complemented and corrected by Fields (1957) and Pascual (1967), the family is subdivided into 4 or 5 subfamilies: Potamarchinae (including the oldest known representatives of the family, extending with doubts from the middle Miocene to the early Pliocene); Gyriabrinae (late Miocene to late Pliocene); Dinomyinae (including only the extant *D. branickii*); Eumegamyinae (late Miocene to the late Pliocene, including the largest representatives of the family); and Tetrastylinae (late Miocene to late Pliocene), considered by many authors as a subgroup of the Eumegamyinae or Dinomyinae (Fields 1957). Although this systematic scheme gives some stability to the >60 fossil species described (Kraglievich 1926, 1930; Mones 1986), knowledge of the anatomy of these animals is insufficient due to the lack of

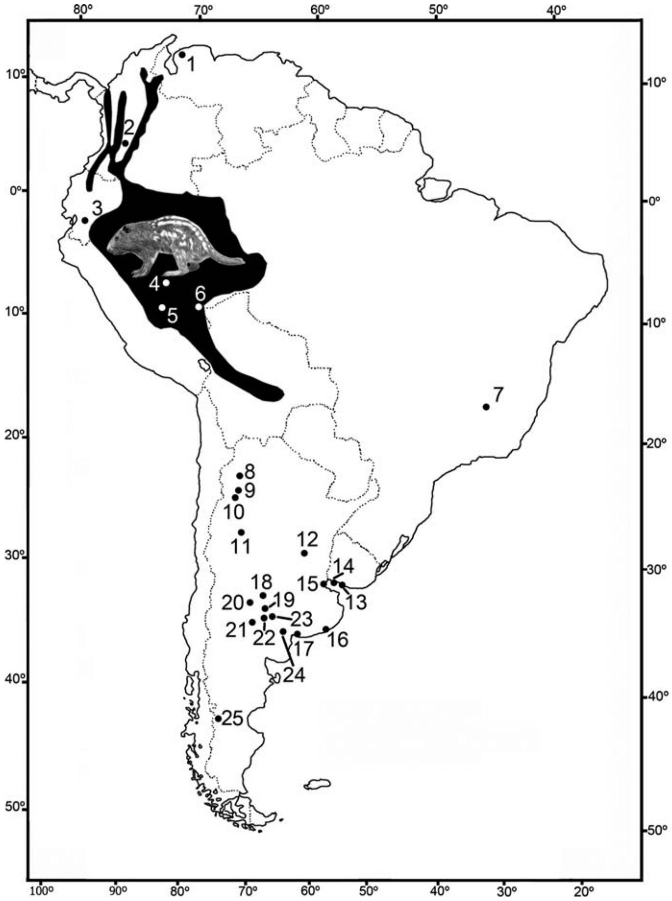


FIG. 1.—Map of South America showing the approximate current distribution of *Dinomys branickii* (black) and the locations (numbers) with fossil record of the Dinomyidae (compiled from several sources). 1, Urumaco, Estado Falcón (Venezuela); 2, La Venta (Colombia); 3, Nabón (Ecuador); 4, Alto Río Juruá (Brazil); 5, Fitzcarrald (Peru); 6, Río Acre (Peru/Brazil); 7, Pedro Leopoldo, Lagoa Santa (Brazil); 8, Valle Calchaquí, Salta (Argentina); 9, Río Santa María, Catamarca (Argentina); 10, Puerta de Corral Quemado, Catamarca (Argentina); 11, Sierra de Velasco, La Rioja (Argentina); 12, Cliffs of the Paraná River, Entre Ríos (Argentina); 13, Arazatí and Kiyú, San José (Uruguay); 14, Bahía de Colonia, Colonia (Uruguay); 15, Villa Ballester, Buenos Aires (Argentina); 16, Chapadmalal, Buenos Aires (Argentina); 17, Farola de Monte Hermoso, Buenos Aires (Argentina); 18, Caleufú, La Pampa (Argentina); 19, Toay, La Pampa (Argentina); 20, Telén, La Pampa (Argentina); 21, Cerro La Bota, La Pampa (Argentina); 22, Gamay, La Pampa (Argentina); 23, Salinas Grandes, La Pampa (Argentina); 24, Arroyo Chasicó, Buenos Aires (Argentina); 25, Laguna Blanca, Chubut (Argentina).

associated cranial and postcranial remains. Most specimens consist only of isolated teeth or small fragments of skulls or mandibles (Mones 1986), precluding any possibility of developing a comprehensive comparative analysis of the different lineages in Dinomyidae.

In Uruguay the fossil record of the family is poor and restricted to the southwest portion of the country (Fig. 1). Records began during the 1st half of the 20th century with the discovery and description of a partial palate without clear stratigraphic provenance, assigned to the new species *Gyriabrus teisseirei* by Kraglievich (1930). Later, Francis and Mones (1966) described *Josephoartigasia magna* (Mones 2007) based on a reworked jaw fragment bearing part of the dental series and an isolated incisor of presumed late Pliocene age, tentatively ascribed to the San José Formation (currently Raigón Formation—Tofalo et al. 2009). Calcaterra (1972) proposed the presence of *Eumegamys* sp. based on a reworked incisor fragment recovered from the coast of El Real de San Carlos, Colonia Department. Mones and Castiglioni (1979) recognized the new species *Isostylomys intermedius* based on a single premolar collected in the late Miocene sediments of the Camacho Formation, San José Department. Finally, recent revisions of the materials deposited in the collection of the Museo Nacional de Historia Natural (MNHN) have contributed to the knowledge of the anatomy of the group: Rinderknecht (pers. obs.) reported the 1st articulated postcranial remains known for a eumegamyine; Rinderknecht and Blanco (2008) described the well-preserved skull of *J. monesi*; and Bostelmann (pers. obs.) presented the 1st associated craniomandibular remains of the genus *Isostylomys*, addressing some aspects of dental development in eumegamyines.

In this report we describe the skull, dentition, and atlas of a new genus and species of late Miocene Dinomyidae from Uruguay, which comprise one of the best preserved fossils of this group of giant rodents. Also, we discuss briefly several aspects of the auditory region in Dinomyidae to provide new evidence about their potential taxonomic value in the characterization of previously described genera and species, until now almost totally based on dental characters.

MATERIALS AND METHODS

The holotype specimen is located in the MNHN, Montevideo, Uruguay (MNHN 2521). Anatomical terminology used in this paper follows Van der Klaauw (1931), Hill (1935), Lessertisseur and Saban (1967), Pascual (1967), and Patterson and Wood (1982). We concur on the taxonomic placement of species allocated to the genus *Olenopsis* from La Venta, Colombia, and Paraná, Argentina, into *Drytomomys*, as has been proposed recently by Candela and Nasif (2006) in their review of the genus. The characteristics discussed for the basicranial region of the genus *Eumegamys* are based on the observed condition in the material MACN 4006 assigned to this genus by Kraglievich (1926). In the light of our findings we recommend that this assignment needs to be revised in future analysis. We followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). All the specimens examined that were used in the comparisons and the institutional abbreviations are listed in Appendix I.

RESULTS

SYSTEMATICS

Order Rodentia Bowdich, 1821
Family Dinomyidae Alston, 1876
Subfamily Eumegamyinae Kraglievich, 1932
Arazamys, new genus

Type and only species.—Arazamys castiglionii, new genus and species.

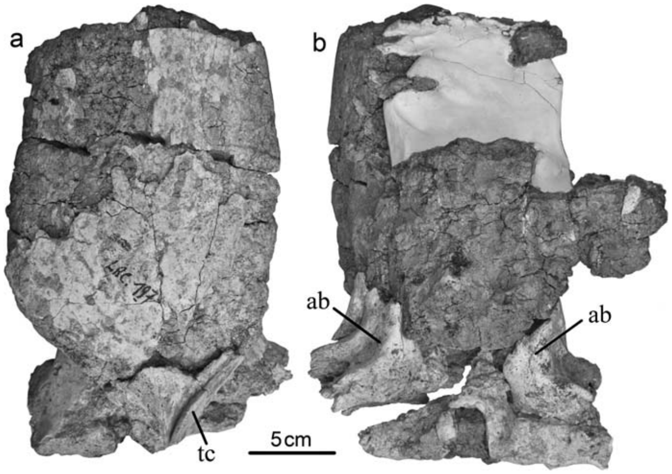


FIG. 2.—Holotype of *Arazamys castiglionii*, new genus and species (MNHN 2521); posterior part of the skull in a) dorsal and b) ventral views. Abbreviations: ab = auditory bullae, tc = right parasagittal crest.

Distribution.—Southern coast of San José Department, Uruguay. Late Miocene, Huayquerian South American Land Mammal Age.

Etymology.—*Araza* = after Arazatí beach, the type locality where the material was collected; *mys* = mouse.

Morphological diagnosis.—Large member of Eumegamyinae, bigger than *Phoberomys* (Neoepiblemidae) but somewhat smaller than the largest representatives of the Dinomyidae (genus *Isostylomys* and *Josephoartigasia*), characterized by having P4, M1, and M2 composed of 5 transverse lophs of which the first 2 (anterior ones) remain free and the 3 posterior ones are joined together on the lingual (internal) side. It differs from all species of *Isostylomys* by having P4 with the last 3 lophs jointed. Also, it differs from *Eumegamys* and *Pentastylodon* by having M1 composed of 5 lophs (4 in *Eumegamys* and 6 in *Pentastylodon*) and from *Eumegamysops* by having M2 composed of 5 lophs. *Arazamys* is the only member of the Eumegamyinae that bears a M3 composed of 5 lophs with the last 2 of them joined together (3 united in *Pentastylodon*).

Auditory region characterized by a short meatus acusticus externus (like *Eumegamysops* and *Eumegamys* and different from *J. monesi*), with a foramen stylomastoideum located below it and a well-developed ectotympanic cavity.

Arazamys castiglionii, new genus and species
Figs. 2–4, 6–8; Table 1

Holotype.—MNHN 2521, posterior region of the skull preserving the braincase, both occipital condyles, and the entire right auditory region. Complete dental series except for the left P4 and part of the right incisor. Well preserved Atlas.

Hypodigm.—The holotype is the only specimen known to date.

Type locality and stratigraphy.—Fossil remains were collected on the Arazatí beach coastal platform in the Department of San José, southwestern Uruguay (34°34′S, 56°58′W; Fig. 1). Three lithostratigraphic units are usually recognized in the outcrops exposed on the coastal cliffs and the littoral platform of San José Department. From the base to the top of the section these are the Camacho (late Miocene), the Raigón (Pliocene to Pleistocene), and the Libertad (Pleistocene) formations (Bossi and Navarro 1991; Tófalo et al. 2009).

In Arazatí the sediments of the Camacho Formation represent the first 2–5 m of the base of the cliffs and the exposed littoral platform at sea level (Perea and Martínez 2004; Sprechmann et al. 2000). Field observations indicate that the sediments continue into the Río de La Plata, although the extent and thickness under the surface of the water are unknown (Sprechmann et al. 2000). For some authors this lithofacies represents an independent unit, the Kiyú Formation (Francis and Mones 1965), or the base of the Raigón Formation (Bossi and Navarro 1991). Sprechmann et al. (2000), while discussing the lithology of the Camacho Formation in the area, proposed the recognition of this local unit as the Kiyú lithofacies.

The sediments of the Camacho Formation are composed of conspicuous greenish gray friable and moderately compacted pelite that becomes greenish-brownish toward the top of the formation in its contact with the superposed Raigón Formation. This sedimentation episode probably represents a late Miocene transgressive event. The facies includes oyster patch reefs and incrusted ichnofossils such as *Ophiomorpha nodosa* and *Thalassinoides* sp. (Sprechmann et al. 1998, 2000), and vertebrates such as fishes, freshwater turtles, estuarine birds, and an abundant record of terrestrial mammals (Perea 2005). The holotype of *A. castiglionii* was recovered from the greenish sandy pelite a few meters above the shoreline of the Río de la Plata in the Kiyú lithofacies of the Camacho Formation (Sprechmann et al. 2000). This unit is chronobiostratigraphically assigned to the late Miocene Huayquerian South American Land Mammal Age (Perea and Martínez 2004), as is suggested by its fossil mammal assemblage that includes marsupial carnivores, xenarthrans, hystricognath rodents, notoungulates, litopterns, and cetaceans (Perea 2005; Perea et al. 1994). The presence of a terrestrial fauna embedded with estuarine and marine oysters, fish remains, turtles, and flamingoes is considered to be the result of transport into a paralic environment, possibly including coastal lagoons and floodplains in an estuarine or deltaic system (Perea 2005; Perea et al. 1996; Ubilla et al. 1990). Skeletal remains frequently appear with some degree of articulation between bones and with a low degree of weathering and deformation, allowing us to suppose limited transport and quick burial after deposition. The presence of disarticulated bones in addition to partially articulated skeletons also supports the hypothesis of a parauthochthonous origin for these faunas.

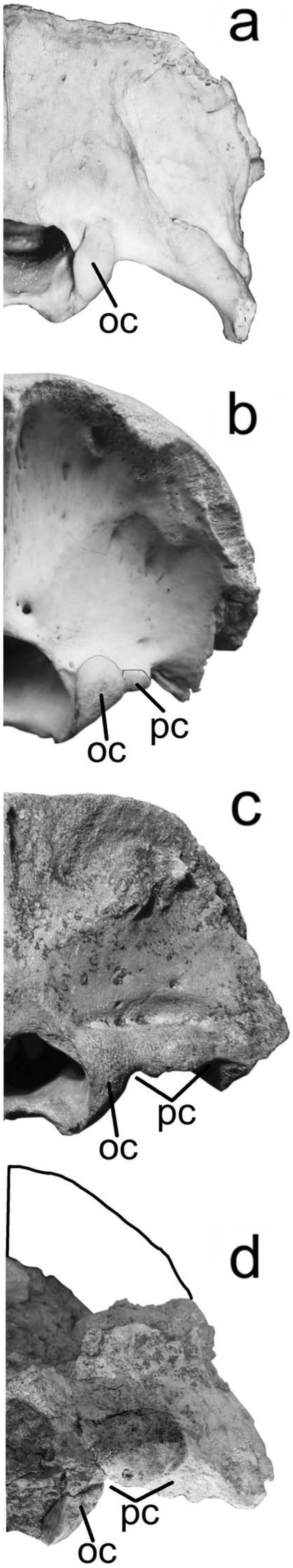
Etymology.—In honor of Luis Castiglioni, Uruguayan amateur paleontologist who collected the type material and several other remarkable fossils during the last 3 decades.

Description and Comparison

Skull.—Only the rear half of the skull has been preserved, which includes much of the frontal and parietal bones all solidly fused together. Two parasagittal crests are visible in dorsal view and as in all representatives of the family Dinomyidae are remarkable for their great development. Although the most posterior region of the skull has not been preserved, we assume that these 2 crests joined each other, forming a short sagittal crest (see Fig. 2a). In posterior view the well-developed occipital condyles can be seen. The foramen magnum is subcircular and lies perpendicular to the nuchal plane.

A pair of extra articular extensions called paracondyles or accessory condyles (Ameghino 1916; Burmeister 1885) are positioned in the nuchal plane at the external lateral side of each of the occipital condyles (Fig. 3). In posterior view they form 2 well-defined articular sheets of slightly convex subcircular outline, connected to the occipital condyles through a flat surface. These unique structures do not exist in any other group of mammals and are of great systematic importance because their presence is a diagnostic feature of the Dinomyidae (including *D. branickii*) and clearly separates them from other giant rodents such as the Hydrochoeridae, Neoepiblemidae, and ''Heptaxodontidae'' (Ameghino 1916; Horovitz et al. 2006; Mones 1997; Negri and Ferigolo 1999; Rinderknecht and Blanco 2008). Compared with other Dinomyidae (*D. branickii*, *Josephoartigasia*, *Drytomomys*, *Telicomys*, *Tetrastylus*, *Eumegamysops praependens*, MACN 4006, and MACN 4007) from which these structures are also known, in *Arazamys* they are more rounded and with a larger surface. Above each of the paracondyles is a depression for the dorsal edge of the atlas. Although the function of the paracondyles is uncertain (Ameghino 1916; Mones 1997), the existence of these accessory articular facets, in conjunction with the development of a marked occipital fossa for the atlas, indicates that the articulation of the 1st vertebra with the skull was extremely solid.

The auditory bullae are small in proportion to the size of the skull (Fig. 2b), kidney-shaped and not inflated, as characteristically observed in Eumegamyinae (in contrast with the condition present in the remaining subfamilies that possess inflated auditory bullae). The meatus acusticus externus forms a short tube of circular cross section (Fig. 4c). As in some Eumegamyinae, an excavated pit or cavity is located anterior to the meatus acusticus externus. Despite an exhaustive search in the classical anatomical literature, we were unable to find a description or a suggested nomenclature for this particular



←

Fig. 3.—Right occipital region (nucal plane, not to scale) of a) *Lagostomus maximus* (MNHN comp-207), b) *Dinomys branickii* (MNHN 3796), c) *Eumegamysops praependens* (MLP 41XII-13-237), and d) holotype of *Arazamys castiglionii*, new genus and species (MNHN 2521, reversed side). oc = occipital condyle, pc = paracondyle.

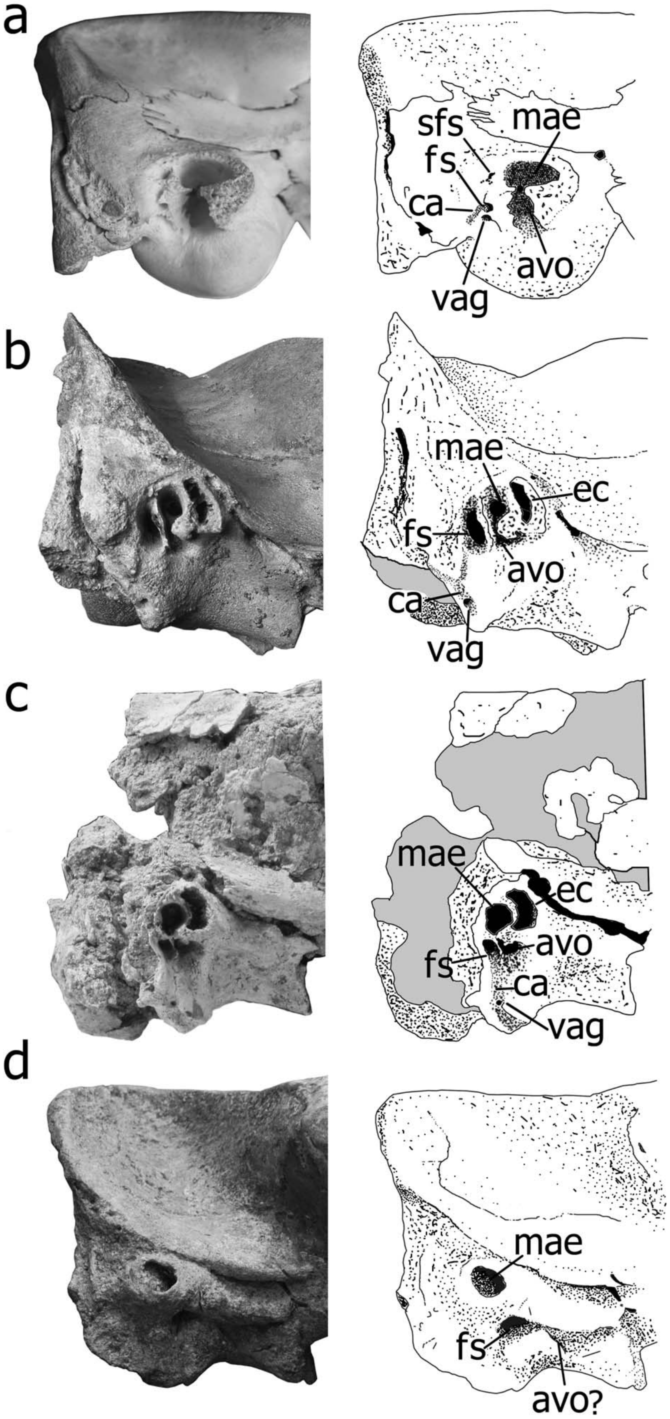


Fig. 4.—Right auditory region (not to scale) of a) *Dinomys branickii* (MNHN 3796, reversed side), b) *Eumegamysops praependens* (MLP 41XII-13-237), c) holotype of *Arazamys castiglionii*, new genus and species (MNHN 2521), and d) *Josephoartigasia monesi* (MNHN 921). avo = accessory ventral opening, ca = canal between foramen stylomastoideum and vagina processus hyoidei, ec = ectotympanic cavity, fs = foramen stylomastoideum, mae = meatus acusticus externus, sfs = secondary foramen stylomastoideum, vag = vagina processus hyoidei.

Table 1.—Dental measurements (in mm) of *Arazamys castiglionii*, new genus and species (MNHN 2521).

	Mesiodistal length	Buccolingual width
Right P4	22.9	20.5
Right M1	25.0	20.7
Right M2	24.8	19.2
Right M3	26.7	19.1
Left P4	—	—
Left M1	21.1	20.4
Left M2	25.1	19.0
Left M3	26.3	19.8
Right I	—	25.4
Left I	210.0	25.6

cavity or any similar structure. Faced with this dilemma we propose here to name it ectotympanic cavity, considering that a more inclusive review of the mammalian ear region might confirm the uniqueness of this anatomical structure. A detailed description of the cavity is offered in the next section. Below this ectotympanic cavity an accessory ventral opening is observed. The foramen stylomastoideum is located just below the meatus acusticus externus and is notable for its great development. Under the foramen stylomastoideum a canal that joins this foramen with a small circular groove is observed that we interpret as an attachment surface for articulation of the tympanohyal bone of the hyoid arch. The groove corresponds to the vagina processus hyoidei described by Van der Klaauw (1931) in several mammals (Fig. 4).

Due to the imperfect state of preservation of the mastoid bone, it is not possible to determine whether a secondary foramen stylomastoideum was present. Among the Dinomyidae some forms such as *Dinomys*, *Tetrastylus*, and possibly *Drytomomys* do present this secondary foramen (Figs. 4 and 5). As in all members of the subfamily Eumegamyinae, the foramen jugular (= foramen metoticum) of *Arazamys* is located in a retrotympanic fossa (Fernández de Alvarez 1958; Pascual 1967).

Dentition.—The dentition of *Arazamys* has been preserved almost completely except for the left P4 and part of the right incisor (Figs. 6 and 7). As frequently happens in the Dinomyidae, the grinding teeth in *Arazamys* are small relative to the estimated size of the skull and the great development of the incisors (Rinderknecht and Blanco 2008).

The robust incisors, from which only the anterior enamel band is retained, are pale orange in color, lack marked grooves, and present tiny striations that can be seen along the entire length of each tooth. The teeth are curved in lateral view, but the enamel band itself is flat.

All the molars of the cheek-tooth series are similar in size (with P4 the shortest and M3 the longest of the series), hypselodont, and consist of 5 lophs or transverse sheets of dentine surrounded by a thin band of enamel—almost imperceptible in the back of each loph—and separated by a narrow layer of cement. Although the union pattern between the lophs varies with each tooth, when it occurs it is always at

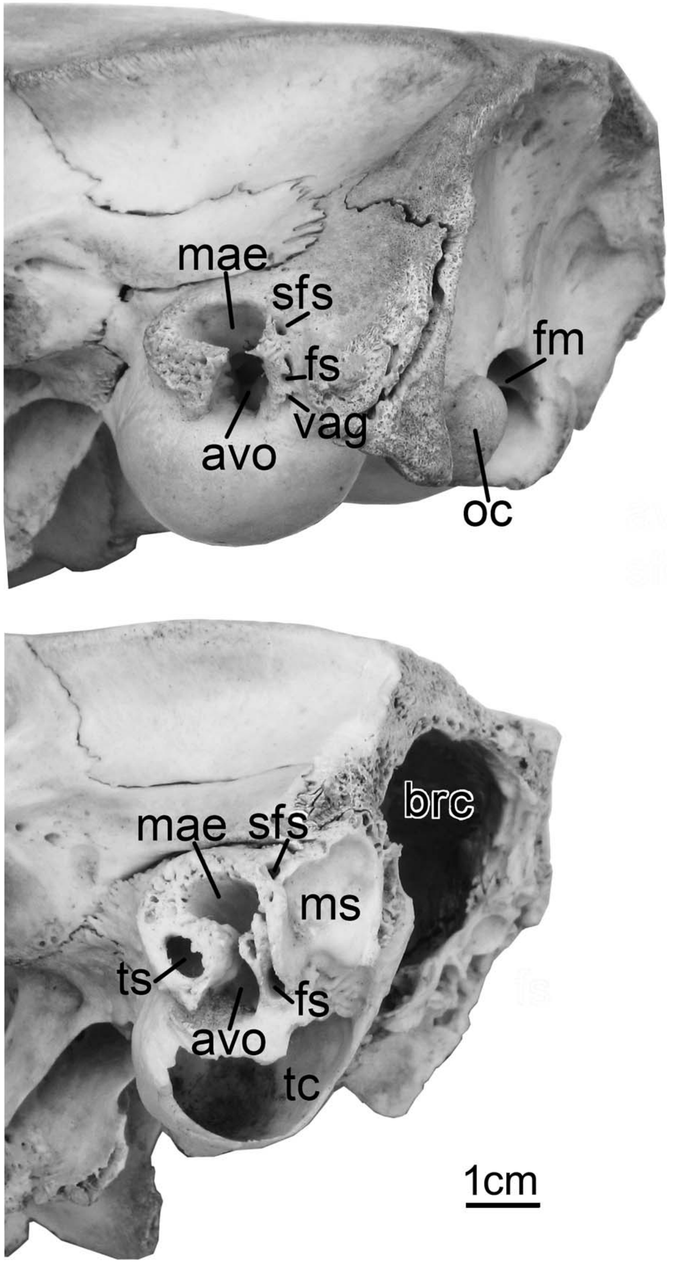


FIG. 5.—Left auditory region of *Dinomys branickii* showing the external (top, MNHN 3796) and internal (bottom, MNHN 3795) morphology. avo = accessory ventral opening, brc = braincase, fs = foramen stylomastoideum, fm = foramen magnum, mae = meatus acusticus externus, ms = mastoid sinus, oc = occipital condyle, sfs = secondary foramen stylomastoideum, tc = tympanic cavity, ts = tympanic sinus, vag = vagina processus hyoidei.

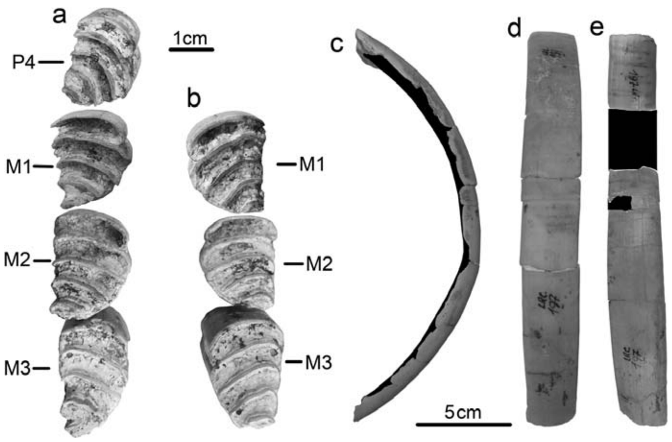


FIG. 6.—Holotype of *Arazamys castiglionii*, new genus and species (MNHN 2521); a) right P4–M3 in occlusal view, b) left molar series in occlusal view, left incisor in c) lateral and d) anterior views, and e) right incisor in anterior view.

the lingual side. The occlusal surface on each tooth is almost flat with the labial and lingual borders equally worn.

The P4 is triangular in occlusal view and composed of 5 transverse lophs with marked curvature. The 2 anterior lophs remain free, and the 3 posterior ones are joined together along the lingual side. As in other representatives of the Eumegamyinae, the 1st loph has a transverse width significantly narrower than the rest of the lophs in the tooth (Fig. 6). M1 and M2 possess a conformation similar to that of P4, with 2 free anterior lophs and 3 posterior ones joined lingually. These teeth differ from P4 by presenting less curved lophs, and the 1st loph of each tooth is less reduced in transverse width. M3 is composed of 3 free anterior lophs and 2 smaller posterior lophs that also are united lingually.

Atlas.—The atlas is the only preserved postcranial bone and is characterized by its robustness and the presence of an extra pair of articular facets for the paracondyles (Fig. 8). The neural spine has not been preserved, but a detailed study of this region suggests that it was very small. In frontal view the neural canal presents a subelliptical shape that becomes an inverted bell in posterior view. On both sides the maximum transverse width is achieved in its dorsal portion. Given the fragile state of the bone, it has not been possible to remove the sediments that fill this cavity. The transverse processes are not preserved. The paracondylar articular facets are well developed and extend laterally. They are concave, subtriangular, anteriorly projected, and separated by a tenuous ridge from the occipital facets. The articular facets for the occipital condyles are concave and less elongated longitudinally than in their transverse axis. The articular facets for the axis are nearly flat. The transverse foramina are covered with matrix, precluding their description. The degree of fusion of the sutures of the

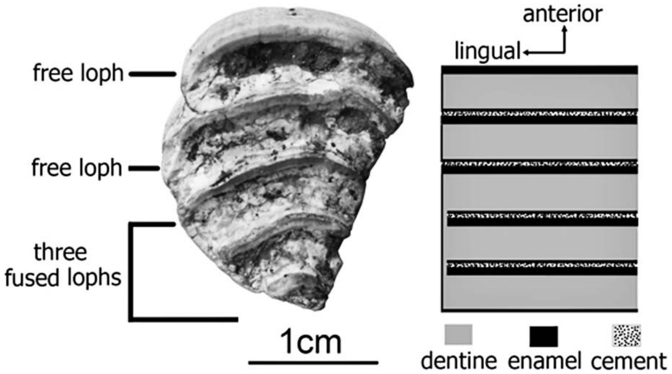


FIG. 7.—Occlusal view of the left M1 of *Arazamys castiglionii*, new genus and species (MNHN 2521).

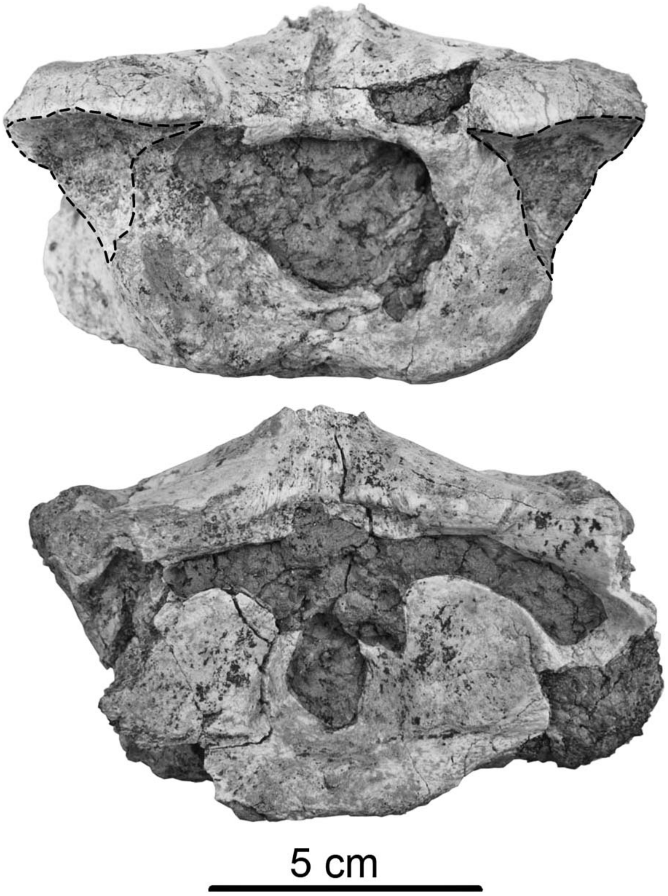


Fig. 8.—Atlas of *Arazamys castiglionii*, new genus and species (MNHN 2521), in anterior (top) and posterior (bottom) views. Dashed lines show the articulation surfaces for paracondyles.

atlas indicates that the specimen was an adult at the time of death (Fig. 8).

Discussion

Historically the taxonomy and systematics of fossil Dinomyidae have relied solely on attributes of cranial morphology (Kraglievich 1926, 1930). Until now the main characteristics used to define the different groups (subfamilies) have been the number of lophs that compose each tooth, the confluences among the lophs on each tooth, the lingual morphology of each of the lophs, the degree of hypsodonty of the teeth, the presence or absence of a sagittal crest, the morphological patterns of the auditory bullae, and the presence of a pretympanic fossa and a retrotympanic fossa (Fields 1957; Kraglievich 1926, 1930; Pascual 1967). Of these traits, the vast majority of the descriptions of genera and species rely almost completely on the attributes of the dental series and in a few exceptional cases even on the morphological particularities observed in just one single tooth (i.e., *Doellomys parcus*, *Pentastylomys racedi*, and *Protomegamys coligatus*). The real value of the dental topology as a robust character set for taxonomic purposes remains to be demonstrated by a detailed study on the homologies and the ontogenetic development of dental traits in the entire family.

Following the suprageneric-level traditional classifications (Pascual 1967), *Arazamys* should be included within the subfamily Eumegamyinae based on its enormous size, the shape and composition of the tooth lophs, its kidney-shaped and proportionately small bulla, and the presence of a sagittal crest. Unfortunately, the existence of a pretympanic fossa (present only in Eumegamyinae—Pascual 1967; Rinderknecht and Blanco 2008) cannot be demonstrated in our material because of the lack of preservation of the area where the fossa is located. It is important to clarify that given the fragmentary nature of the fossil record, many of the extradental features that have traditionally been used to diagnose subfamilies within Dinomyidae cannot be tested in all described genera and species. This is, for example, the case of the Potamarchinae and Gyriabrinae, from which a complete braincase has never been published. The only genera of the almost 20 described for the whole family in which nearly complete skulls are preserved are *Dinomys* (the living representative of Dinomyinae), *Telicomys*, *Tetrastylus* (Rovereto 1914), *Eumegamysops* (Fernández de Alvarez 1947, 1958), and *Josephoartigasia* (both of them joined in the Eumegamyinae). This fundamental restriction highlights the importance of the dental series as a necessary element for present taxonomic use when describing or referring new specimens. Following this reasoning, *Arazamys* is placed in the subfamily Eumegamyinae because all upper molars are composed of more than 4 lophs (unlike Tetrastylinae and Dinomyinae), which never join at the labial side (unlike Potamarchinae and Gyriabrinae). Within Eumegamyinae *Arazamys* is the only taxon that has an M3 with only 2 lophs united lingually (see Fig. 6). It is also important to note that P4, M1, and M2 have an identical conformation; each is formed by 5 lophs, with the 3 posteriormost ones joined lingually, a condition only previously recorded in the genus *Josephoartigasia* of the Pliocene of Uruguay. The latter and *Arazamys* differ in tooth morphology only in the existence of a small extra loph in M3 in the former.

Despite being one of the best preserved Dinomyidae, *Arazamys* (as any other dinomyid known so far) must be diagnosed 1st by dental morphology, because features such as the shape of the auditory bulla or the presence of a pretympanic fossa cannot be used reliably in the systematics of the Dinomyidae until complete skulls of the Potamarchinae and Gyriabrinae are described. Nevertheless, cranial morphology and specifically the auditory region do help in the characterization of forms at the generic and some suprageneric levels, for example, supporting distinctions between members of the Dinomyinae, Tetrastylinae, and Eumegamyinae, or separating genera within the Eumegamyinae themselves. As we note in the following paragraphs, this distinction could be of great interest in the search for additional phylogenetically informative characters within the Dinomyidae.

Although the auditory region of Eumegamyinae presents very peculiar characteristics, it is known from only just 3 genera (*Eumegamysops*, *Eumegamys*, and *Josephoartigasia*) and has never been studied in detail. One of the most remarkable features of this region is the existence in some Eumegamyinae (including *Arazamys*) of the ectotympanic cavity positioned anterior to the meatus acusticus externus (Fig. 4). Our studies show that this cavity is not a false or external auditory meatus or meatus acusticus externus spurius (Van der Klaauw 1931), because it is delimited uniquely by the ectotympanic bone without involvement of the postglenoid process. The location of this cavity (anterior to the meatus acusticus externus) also precludes the possibility that it represents a foramen supratympanicum or a sinus epitympanicum. In *Dinomys* hollow cavities without external communication (tympanic sinuses) are located in the ectotympanic bone anterior to the meatus acusticus externus (Fields 1957; Fig. 5). We believe that this cavity is actually part of these sinuses, which in many Eumegamyinae reach such a pronounced development that they join one another, communicating with the outside. A small foramen in the inner wall of the ectotympanic cavity of Eumegamyinae (whose function is unknown to us) also is present in the innermost region of the tympanic sinuses of *Dinomys* (see Fig. 5). This leaves little doubt about the homology of these 2 structures, at least for *Dinomys* and the Eumegamyinae. Putative origin of the ectotympanic fossa from the tympanic sinuses also enables us to propose that the interpretation of that structure as a part of the meatus acusticus externus is incorrect (Fernández de Alvarez 1958).

The auditory region of *Arazamys* follows the general pattern of the auditory region in Eumegamyinae, with a short meatus acusticus externus, a highly developed foramen stylomastoideum, and the presence of an ectotympanic cavity. Nevertheless, the arrangement of these structures differs from the condition observed in other members of the subfamily. In *Eumegamysops* the foramen stylomastoideum is located behind the meatus acusticus externus, whereas in *Arazamys* it lies just below the meatus. On the other hand, the accessory ventral opening in *Eumegamysops* is located below the meatus acusticus externus, whereas in *Arazamys* it is located below the ectotympanic cavity. Finally, the canal that connects the foramen stylomastoideum with the vagina processus hyoidei is nearly perpendicularly oriented in *Arazamys*, but in *Eumegamysops* this channel is directed toward the posterior region of the skull, becoming subdivided into 2 channels. The conformation of the auditory region in *Eumegamysops* is indistinguishable from that in the specimen MACN 4006 assigned to *Eumegamys* by Kraglievich (1926). Although the differences at the level of the auditory region between *Arazamys* and *Eumegamysops* are remarkable, both taxa show the general pattern described for the auditory region in Eumegamyinae. However, this general pattern is not present in the auditory region of *Josephoartigasia*, which clearly differs from *Arazamys*, *Eumegamys*, and *Eumegamysops*. In *Josephoartigasia* the ectotympanic cavity is absent, and the meatus acusticus externus is a long tube that projects into the posterior region of the skull (Fig. 4d). This tubular structure resembles the one present in the family Chinchillidae and demonstrates that within the Eumegamyinae taxa that present similar dental morphologies (such as *Arazamys* and *Josephoartigasia*) can display significant differences in the auditory region.

In summary, our investigation indicates that the auditory region clearly exhibits a set of characters with potentially diagnostic value in the Dinomyidae, something that in the current state of knowledge is not possible to fully assess given the fragmentary nature of the specimens of almost all of the genera and species described (which as has been noted, are mostly based on dental or mandibular remains). In this sense, although the composition and pattern of the lophs in the dental series seem to be a reasonable enough basis on which to erect a new genus or species, the elucidation of the phylogenetic relationships along the Dinomyidae and certainly within Eumegamyinae is an unsolved problem whose answer depends on the discovery of reasonably complete cranial remains.

RESUMEN

Se describen restos fósiles de un nuevo género de roedor gigante: *Arazamys castiglionii* (Mammalia, Rodentia, Dinomyidae), colectados en la costa de la Playa Arazatí (Departamento de San José, sur de Uruguay). Los materiales fueron exhumados de sedimentos pelíticos asignados a la Formación Camacho del Mioceno tardío, bioestratigráficamente correlacionados a la Edad Mamífero Huayqueriense. El material tipo consta de un atlas y el cráneo incompleto el cual preserva la caja craneana, la región auditiva y ambas series dentarias (exceptuando al P4 izquierdo y parte del incisivo derecho). La presencia de 5 lofos en el P4, M1, M2 y M3, en conjunto con el patrón de unión interlofos en cada uno de los dientes permite caracterizar a *Arazamys* como un nuevo género dentro de los Eumegamyinae. A partir de estudios comparativos de la anatomía de la región auditiva se describen 2 morfologías para Eumegamyinae; una caracterizada por presentar el meatus acusticus externus corto, un gran desarrollo del foramen stylomastoideum y una conspicua cavidad ectotimpánica y otra, caracterizada por presentar un meatus acusticus externus largo y carecer de fosa ectotimpánica. El potencial valor taxonómico y sistemático de la región auditiva en Dinomyidae es discutido a la luz de estos resultados.

ACKNOWLEDGMENTS

We express our gratitude to P. Jenkins, M. Reguero, and A. Kramarz, who allowed access to the collections under their care. D. Croft and P. Higgins provided dedicated help and made insightful comments that clearly improved the manuscript. A. Candela, C. Vieytes, N. Nasif, and M. G. Vucetich provided us with technical literature, images, and information about their current investigations on caviomorph rodents. Two anonymous reviewers made useful corrections and shared their points of view on specific topics, helping us to refine some sections of the manuscript. To all of them we express our deepest gratitude. This work was supported by the Agencia Nacional de Investigación e Innovación and Pedeciba–Biología, Uruguay.

LITERATURE CITED

Alston, E. R. 1876. On the classification of the order Glires. Proceedings of the Zoological Society of London 1876:67–98.

Ameghino, C. 1916. Algunas observaciones curiosas sobre una cabeza del género *Tetrastylus* de Catamarca. Physis 2:429–430.

Ameghino, F. 1883a. Sobre una colección de mamíferos fósiles del piso mesopotámico de la formación patagónica, recogidos en las barrancas del Paraná, por el profesor Pedro Scalabrini. Boletín de la Academia Nacional de Ciencias en Córdoba 5:101–116.

Ameghino, F. 1883b. Sobre una nueva colección de mamíferos fósiles recogidos por el Profesor Scalabrini en las barrancas del Paraná. Boletín de la Academia Nacional de Ciencias en Córdoba 5:257–306.

Ameghino, F. 1885. Nuevos restos de mamíferos fósiles oligocenos recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo Provincial de la Ciudad del Paraná. Boletín de la Academia Nacional de Ciencias en Córdoba 8:5–207.

Ameghino, F. 1886. Contribuciones al conocimiento de los mamíferos fósiles de los terrenos terciarios antiguos del Paraná. Boletín de la Academia Nacional de Ciencias en Córdoba 9:5–228.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas de la Academia Nacional de Ciencias 6:xxxii, 1–1027.

Ameghino, F. 1891a. Caracteres diagnósticos de cincuenta especies nuevas de mamíferos fósiles argentinos. Revista Argentina de Historia Natural 1:129–167.

Ameghino, F. 1891b. Mamíferos y aves fósiles argentinas. Especies nuevas, adiciones y correcciones. Revista Argentina de Historia Natural 1:240–259.

Blanco, R. E. 2008. The uncertainties of the largest fossil rodent. Proceedings of the Royal Society of London, B. Biological Sciences 275:1957–1958.

Bondesio, P. 1978. La presencia del género *Carlesia* (Rodentia, Dinomyidae, Eumegamyinae) en la formación Arroyo Chasicó (Plioceno Temprano), Provincia de Buenos Aires. Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata ''Lorenzo Scaglia'' 2:198–206.

Bossi, J., and R. Navarro. 1991. Geología del Uruguay. Departamento de Publicaciones de la Universidad de la República, Montevideo, Uruguay.

Bowdich, T. E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith, Paris, France.

Burmeister, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. Anales del Museo Público, Buenos Aires 3:95–174.

Calcaterra, A. 1972. Dos roedores fósiles nuevos para Uruguay y confirmación de otro. Comunicaciones Paleontológicas del Museo Nacional de Historia Natural de Montevideo 1:11–21.

Candela, A., and N. L. Nasif. 2006. Systematics and biogeographic significance of *Drytomomys typicus* (Scalabrini in Ameghino, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from Northeast of Argentina. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 3:165–181.

Collins, L. R., and J. F. Eisenberg. 1972. Notes on the behaviour and breeding of pacaranas (*Dinomys branickii*) in captivity. International Zoo Yearbook 12:108–114.

Fernández de Alvarez, E. 1947. Nota preliminar sobre nuevos roedores ''Eumegamyidae.'' Revista de la Asociación Geológica Argentina 2:59–64.

Fernández de Alvarez, E. 1958. Sobre nuevos restos de *Eumegamysops praependens* (Amegh.) Kragl. Revista de la Asociación Geológica Argentina 13:87–104.

Fields, R. W. 1957. Hystricomorph rodents from the late Miocene of Colombia, South America. University of California Publications in Geological Sciences 32:273–404.

Francis, J. C., and A. Mones. 1965. Sobre el hallazgo de *Cardiatherium talicei* n. sp. (Rodentia, Hydrochoeridae) en la Playa Kiyú, Departamento de San José, República Oriental del Uruguay. Kraglieviana 1:3–44.

Francis, J. C., and A. Mones. 1966. *Artigasia magna* n. g., n. sp. (Eumegamyinae), un roedor gigantesco de la época Pliocena superior de las barrancas de San Gregorio, Departamento de San José, República Oriental del Uruguay. Kraglieviana 1:89–100.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Hill, J. E. 1935. The cranial foramina in rodents. Journal of Mammalogy 16:121–129.

Horovitz, I., M. R. Sánchez-Villagra, T. Martin, and O. A. Aguilera. 2006. The fossil record of *Phoberomys pattersoni* Mones 1980 (Mammalia, Rodentia) from Urumaco (late Miocene, Venezuela), with an analysis of its phylogenetic relationships. Journal of Systematic Paleontology 4:239–306.

Kraglievich, L. 1926. Los grandes roedores terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. Anales del Museo Nacional de Historia Natural 34:121–135.

Kraglievich, L. 1930. Descripción de un interesante roedor eumegámido descubierto en el Uruguay. *Gyriabrus teisseirei*, n. sp. Revista de la Sociedad de Amigos de la Arqueología 4:219–224.

Kraglievich, L. 1932a. Diagnosis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina. Rectificación genérica de algunas especies conocidas y adiciones al conocimiento de otras (first part). Anales de la Sociedad Científica Argentina 114:155–181.

Kraglievich, L. 1932b. Diagnosis de nuevos géneros y especies de roedores cávidos y eumegámidos fósiles de la Argentina. Rectificación genérica de algunas especies conocidas y adiciones al conocimiento de otras (second part). Anales de la Sociedad Científica Argentina 114:211–237.

Lessertisseur, J., and R. Saban. 1967. Squelette axial. Pp. 584–708 in Traité de zoologie (P. P. Grassé, ed.). Masson et Compagnie, Paris, France.

Millien, V. 2008. The largest among the smallest: the body mass of the giant rodent *Josephoartigasia monesi*. Proceedings of the Royal Society of London, B. Biological Sciences 275:1953–1955.

Mones, A. 1986. Palaeovertebrata Sudamericana. Catálogo sistemático de los vertebrados fósiles de América del Sur. Parte I. Lista preliminar y bibliografía. Courier Forschungsinstitut Senckenberg 82:1–625.

Mones, A. 1997. Estudios sobre la familia Dinomyidae, II. Aportes para una osteología comparada de *Dinomys branickii* Peters, 1873 (Mammalia: Rodentia). Comunicaciones Paleontológicas del Museo Nacional de Historia Natural de Montevideo 29:1–40.

Mones, A. 2007. *Josephoartigasia*, nuevo nombre para *Artigasia* Francis & Mones, 1966 (Rodentia, Dinomyidae), non *Artigasia* Christie, 1934 (Nematoda, Thelastomatidae). Comunicaciones Paleontológicas del Museo Nacional de Historia Natural de Montevideo 36:213–214.

Mones, A., and L. R. Castiglioni. 1979. Additions to the knowledge on fossil rodents of Uruguay (Mammalia: Rodentia). Paläontologische Zeitschrift 53:77–87.

NEGRI, F. R., AND J. FERIGOLO. 1999. Anatomía craneana de *Neoepiblema ambrosettianus* (Ameghino, 1889) (Rodentia, Caviomorpha, Neoepiblemidae) do Mioceno superior–Plioceno, Estado do Acre, Brasil, e revisão das espécies de gênero. Boletim do Museu Paraense Emílio Goeldi 11:1–80.

PASCUAL, R. 1967. Familia Dinomyidae. Pp. 123–127 in Paleontografía Bonaerense (A. V. Borrello, ed.). Vol. 4 (Vertebrata). Comisión de Investigación Científica, La Plata, Argentina.

PATTERSON, B., AND A. E. WOOD. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. Bulletin of the Museum of Comparative Zoology 149:371–543.

PEREA, D. 2005. *Pseudoplohophorus absolutus* n. sp. (Xenarthra, Glyptodontidae), variabilidad en Sclerocalyptinae y redefinición de una biozona del Mioceno superior de Uruguay. Ameghiniana 42:175–190.

PEREA, D., AND S. MARTÍNEZ. 2004. Estratigrafía del Mioceno–Pleistoceno en ellitoral sur-oeste de Uruguay. Pp. 105–124 in Cuencas sedimentarias de Uruguay, Cenozoico (G. Veroslavsky, M. Ubilla, and S. Martínez, eds.). Ediciones DIRAC, Facultad de Ciencias, Montevideo, Uruguay.

PEREA, D., M. UBILLA, S. MARTINEZ, G. PIÑEIRO, AND M. VERDE. 1994. Mamíferos neógenos del Uruguay: la edad mamífero Huayqueriense en el ''Mesopotamiense.'' Acta Geológica Leopoldensia 39:375–389.

PEREA, D., M. UBILLA, AND G. PIÑEIRO. 1996. First fossil record (late Miocene) of *Phrynops* (*P. geoffroanus* complex: Chelidae) from Uruguay: biostratigraphical and paleoenvironmental context. Copeia 2:445–451.

PETERS, W. C. H. 1873. Über *Dinomys*, eine merkwürdige neue Gattung von Nagethieren aus Peru. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1873:551–552.

POCOCK, R. I. 1926. The external characters of a young female *Dinomys branickii* exhibited in the Society's Gardens. Proceedings of the Zoological Society of London 96:221–230.

RINDERKNECHT, A., AND R. E. BLANCO. 2008. The largest fossil rodent. Proceedings of the Royal Society of London, B. Biological Sciences 275:923–928.

ROVERETO, C. 1914. Los estratos araucanos y sus fósiles. Anales del Museo Nacional de Historia Natural de Buenos Aires 25:1–247.

SANBORN, C. C. 1931. Notes on *Dinomys*. Field Museum of Natural History, Zoology Series 18:149–155.

SPRECHMANN, P., A. L. FERRANDO, AND S. MARTÍNEZ. 2000. Estado actual de los conocimientos sobre la Formación Camacho (Mioceno medio–superior, Uruguay). Pp. 47–65 in El Neógeno de Argentina (F. G. Aceñolanza and R. Herbst, eds.). Instituto Superior de Correlación Geológica, Serie Correlación Geológica, Tucumán, Argentina.

SPRECHMANN, P., M. VERDE, S. MARTÍNEZ, AND C. GAUCHER. 1998. Paleoecología y ambientes de sedimentación de bioestromos y ''patch reefs'' de ostreidos, sus endolitos y epibiontes (Formación Camacho, Mioceno medio–superior; Uruguay). Actas II Congreso Uruguayo de Geología 1:205–209.

TÓFALO, O. R., ET AL. 2009. Geological, pedological and paleomagnetic study of the late Cenozoic sedimentary sequence in southwestern Uruguay, South America. Quaternary International 210:6–17.

UBILLA, M., D. PEREA, C. TAMBUSSI, AND E. P. TONNI. 1990. Primer registro fósil de Phoenicoptheridae (Aves: Charadriiformes) para el Uruguay (Mio–Plioceno). Anais da Academia Brasileira de Ciências 62:61–68.

VAN DER KLAAUW, C. J. 1931. The auditory bulla in some fossil mammals with a general introduction to this region of the skull. Bulletin of the American Museum of Natural History 12:1–352.

VUCETICH, M. G., D. H. VERZI, AND J. L. HARTENBERGER. 1999. Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). Comptes Rendus de l'Académie des Sciences, Series IIA. Earth and Planetary Science 329:763–769.

WHITE, T. G., AND M. S. ALBERICO. 1992. *Dinomys branickii*. Mammalian Species 410:1–5.

Submitted 25 March 2010. Accepted 24 August 2010.

Associate Editor was William F. Perrin.

APPENDIX I

Specimens examined.—Acronyms for institutions are as follows: BMNH, British Museum of Natural History, London, United Kingdom; MNHN, Museo Nacional de Historia Natural, Montevideo, Uruguay; MLP, Museo de La Plata, La Plata, Argentina; MACN, Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia,'' Buenos Aires, Argentina.

Josephoartigasia monesi.—Complete skull (holotype) (MNHN 921).

Isostylomys cf. *I. magnus.*—Nearly complete skull and mandibles (MNHN 2187).

Dinomys branickii.—Nearly complete skeleton (MNHN 3795).

Dinomys branickii.—Skull (MNHN 3796).

Dinomys branickii.—Skull (BMNH-34.9.10.191).

Dinomys branickii.—Skull (BMNH-12.1.15.4).

Eumegamysops praependens.—Incomplete skull (MLP 41XII-13-237).

Eumegamysops praependens.—Braincase assigned to *E. praependens* (MACN 4007) by Fernández de Alvarez (1958). Because this material has no associated teeth, the taxonomic assignment is dubious.

Eumegamys paranensis.—Braincase assigned to *E. paranensis* by Kraglievich (1926) (MACN 4006). Because this material has no associated teeth, the taxonomic assignment is dubious.

Telicomys giganteus.—Nearly complete skull (holotype) (MACN 8011).

Tetrastylus intermedius.—Nearly complete skull and mandibles (holotype) (MACN 8323).