

ASTEROMYS PUNCTUS AMEGHINO (RODENTIA, HYSTRICOGNATHI, CAVIOIDEA) FROM THE LATE OLIGOCENE OF PATAGONIA (ARGENTINA) AND THE EARLY EVOLUTION OF CAVIOIDEA *SENSU STRICTO*



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Abstract. *Asteromys punctus* Ameghino was only known from the holotype, found in the Deseadan locality Cabeza Blanca (Chubut Province, Argentina). This species was included in the Family "Eocardiidae" because of its high-crowned cheek teeth and reduction of the mesoflexid-mesofossettoid. In turn, "Eocardiidae", together with Caviidae and Hydrochoeridae, has been regarded as part of Caviioidea *sensu stricto*, a large group of rodents characterized by double heart-shaped occlusal surface, moderate hystricognathy, and short extension of the lower incisors. The aim of this work is to report a new specimen of *Asteromys punctus* found in the Deseadan locality Laguna de Los Machos, Chubut Province, and to discuss the affinities of this taxon within Caviioidea *s.s.* in the context of a recently published phylogenetic analysis. In that analysis, four unambiguous synapomorphies support the inclusion of *A. punctus* within this clade: presence of mandibular foramen below the m3, root of the lower incisors extending up to the level of the posterior lobe of m2, lateral crest dorsally convex and deflecting anterovertrally from the base of the coronoid process, and horizontal crest as a low and broad ridge. Furthermore, the information provided by the holotype and the new material within a phylogenetic framework allows a discussion of the evidence that supports this taxon as the basalmost member of Caviioidea *s.s.*, placing *Asteromys* in a critical position for understanding the early evolutionary history of Caviioidea *s.s.*

Key words. Caviioidea *s.s.*. "Eocardiidae". Deseadan. Patagonia. Phylogeny.

Resumen. *ASTEROMYS PUNCTUS* AMEGHINO (RODENTIA, HYSTRICOGNATHI, CAVIOIDEA) DEL OLIGOCENO TARDÍO DE PATAGONIA (ARGENTINA) Y LA EVOLUCIÓN TEMPRANA DE CAVIOIDEA *SENSU STRICTO*. *Asteromys punctus* Ameghino era conocido sólo por el holotipo que fue encontrado en la localidad Deseadense de Cabeza Blanca (provincia del Chubut, Argentina). Esta especie se incluyó en la familia "Eocardiidae" por la presencia de molariformes de corona alta y reducción del mesoflexido-mesofosetida. A su vez, "Eocardiidae", junto con Caviidae e Hydrochoeridae, fue ubicado dentro de Caviioidea *sensu stricto*, un gran grupo de roedores caracterizado por la presencia de molariformes con la superficie oclusal en forma de doble corazón, histricognatía moderada y escasa extensión de los incisivos inferiores. El objetivo de este trabajo es dar a conocer un nuevo espécimen de *Asteromys punctus* encontrado en la localidad Deseadense de Laguna de Los Machos (Chubut, Argentina) y discutir las afinidades de este taxón dentro de Caviioidea *s.s.* en el marco de un análisis filogenético recientemente publicado. En dicho análisis, cuatro sinapomorfías no ambiguas soportan la inclusión de *A. punctus* dentro de este clado: foramen mandibular ubicado por debajo del m3, raíz de los incisivos inferiores extendida hasta el nivel del lóbulo posterior del m2, cresta lateral convexa dorsalmente, desviándose antero-ventralmente desde la base del proceso coronoides, cresta horizontal presente como un borde bajo y amplio. Además, la información provista por el holotipo y el nuevo material dentro de un marco filogenético, permitió interpretar a este taxón como el miembro más basal de Caviioidea *s.s.*, ubicando a *Asteromys* en una posición crítica para comprender la historia evolutiva temprana de Caviioidea *s.s.*

Palabras clave. Caviioidea *s.s.*. "Eocardiidae". Deseadense. Patagonia. Filogenia.

ASTEROMYS PUNCTUS Ameghino, 1897, was named based on a right mandibular fragment with the incisor and the entire series of molariform teeth, found in the locality of Cabeza Blanca (Chubut Province, Argentina; late Oligocene, Deseadan age; Fig. 1). Ameghino (1897) classified this species within the Family Cephalomyidae based on plesiomorphic characters (*e.g.*, generalized, small sized, and triangular-shaped cheek teeth). Later, Wood and Patterson (1959) provided a detailed description of *A. punctus* and included it in the Fam-

ily Eocardiidae (Ameghino, 1891) based on its high-crowned cheek teeth and reduction of the mesoflexid-mesofossettoid. The former authors placed Eocardiidae, together with Caviidae and Hydrochoeridae, within Caviioidea *sensu stricto*, a large group of rodents characterized by a double heart-shaped occlusal surface, moderate hystricognathy, and short extension of the lower incisors (Patterson and Wood, 1982).

Wood and Patterson (1959) also proposed the division of the Family Eocardiidae into two subfamilies, implying an

early dichotomy. Based on dental morphology, these authors established the Luantinae represented by *Asteromys* and *Luantus* Ameghino, 1898 and the Eocardiinae represented by *Chubutomys* Wood and Patterson, 1959, *Phanomys* Ameghino, 1887a, *Eocardia* Ameghino, 1887b, and *Schistomys* Ameghino, 1887a. The inclusion of the Deseadan *Chubutomys* within eocardiines was based on the presence of high crowns, hypoflexid penetrating more than half of the occlusal surface and more ephemeral fossetts than in luantines. In turn, *Asteromys* was interpreted as the most primitive member of Luantinae. This group was diagnosed by relatively low-crowned cheek teeth, more persistent fossetts/ids, hypoflex/id penetrating up to half of the occlusal surface, absence of cement, and meta-lophulid II lost in m2–m3. Kramarz (2006) supported the idea of a basal dichotomy for eocardiids, although his proposal of the relationships among genera differed from that of Wood and Patterson (1959). More recently, Pérez (2010a,b) and Pérez and Vucetich (2011) conducted a cladistic analysis

based on morphological data and an extensive taxon-sampling of basal forms of Cavioidea *s.s.* that depicted *Asteromys punctus* as the most basal species of this group. These publications, however, discussed the relationships of euhypsodont cavioids closely related to the crown-group of Cavioidea *s.s.* but lacked an explicit discussion of the character evidence that supports the phylogenetic position of *Asteromys punctus* and the basal nodes of Cavioidea *s.s.*

The aim of this work is to report a new specimen herein assigned to *Asteromys punctus* found in the Deseadan locality Laguna de los Machos (Patterson and Pascual, 1968), Chubut Province (central Patagonia; Fig. 1) and to discuss—within a cladistic framework—the characters involved in the early evolution of Cavioidea *s.s.* that support the phylogenetic position of this taxon. The discussion provided here allows to interpret the phylogenetic significance of the morphology described for *Asteromys* and intends to provide a better understanding of the early evolutionary history of Cavioidea *s.s.*

MATERIALS AND METHODS

Taxonomic nomenclature. Patterson and Wood (1982, p. 511) grouped “Eocardiidae,” Caviidae, and Hydrochoeridae in Cavioidea *sensu stricto* (Cavioidea *s.s.*), which together with Dasyproctidae, Cuniculidae (= Agoutidae), and Dinomyidae formed the more inclusive group Cavioidea. However, recent molecular phylogenetic analyses supported the inclusion of Dinomyidae within Chinchilloidea (Opazo, 2005, Poux *et al.*, 2006, Huchon *et al.*, 2007, Blanga-Kanfi *et al.*, 2009, Rowe *et al.*, 2010). We follow the systematic proposal of Patterson and Wood (1982), excluding Dinomyidae. Recent phylogenetic studies of Cavioidea *s.s.* (Pérez, 2010a,b; Pérez and Vucetich, 2011) supported the paraphyly of “Eocardiidae”. Therefore, quotation marks are used for this assemblage of basal cavioids. The crown group of Cavioidea *s.s.* is formed by Caviidae + Hydrochoeridae, excluding the basal forms (*i.e.*, “eocardiids”) (see Appendix 1).

Anatomical nomenclature. Dental nomenclature follows Marivaux *et al.* (2004) and Pérez (2010b). Mandibular nomenclature is modified from Woods (1972) and Woods and Howland (1979) (see Pérez 2010b).

Hypsodonty. The degree of hypsodonty was measured through the hypsodonty index ($H = \text{crown height} / \text{anterior transverse diameter}$; Janis, 1986). The H was calculated in m1 of the holotype of *Asteromys punctus* (MACN-A 52-110), and the lectotype of *Luantus initialis* (MACN-A 52-164), although *L. initialis* is somewhat more worn. Unworn teeth are unknown for these species.

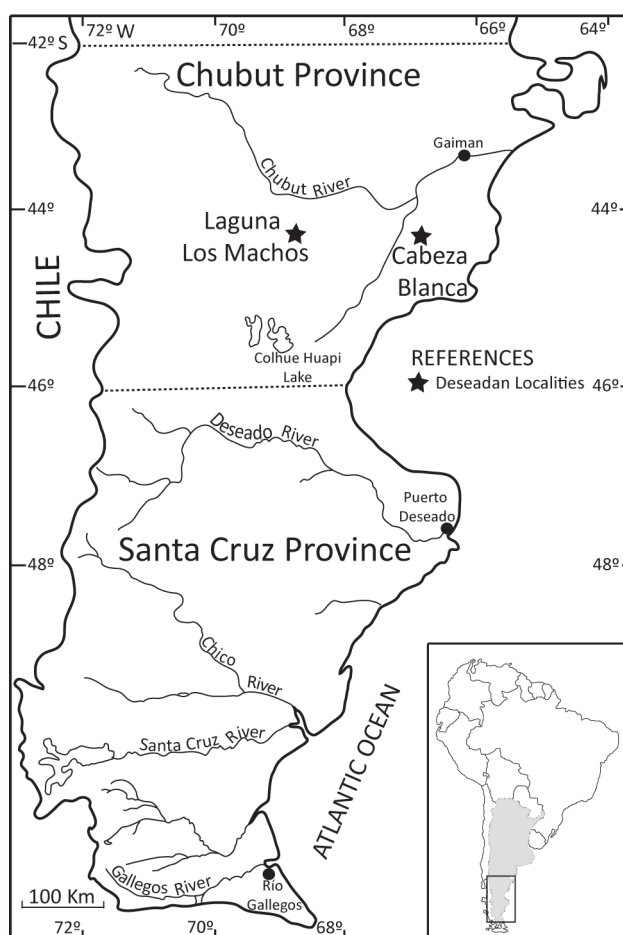


Figure 1. Location map of Cabeza Blanca and Laguna Los Machos localities, Chubut Province, Argentina/ Mapa de ubicación de las localidades Cabeza Blanca y Laguna de Los Machos, provincia del Chubut, Argentina.

Institutional abbreviations. **MACN-A**, Colección Nacional Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **MACN-SC**, Colección Santa Cruz, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **MLP**, Colección de Paleontología de Vertebrados and Colección de Mastozoología, Museo de La Plata, La Plata.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Superfamily CAVIOIDEA Fischer de Waldheim, 1817

Genus **Asteromys** Ameghino, 1897

Type species. *Asteromys punctus* Ameghino, 1897.

Asteromys punctus Ameghino, 1897

Figures 2–3

Expanded diagnosis. *Asteromys* is diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): smallest “eocardiid” with mesodont molars and crowns slightly lower than that of *Luantus initialis* Ameghino, 1902, enamel homogeneous and continuous all around the crown, no cement, persistent fossettids, antero- and metafossettids narrow and long, anterofossettid disappearing before the metafossettid, lingual wall of lower molars straight, hypoflexid wide with round apex opposite the metafossettid, metalophulid II present; *p4 with deep vertical furrow on the anterior side; *anteroposterior length of p4–m1 approximately equal to that of m2–m3; *similar sized lower molariforms.

Holotype. MACN-A 52-110, right mandibular fragment with incisor, p4–m3 and part of the dp4 anterior root (Fig. 2.1–3).

Referred material. MLP 59-II-26-97, left mandibular fragment with incisor, dp4, p4–m3 (Fig. 3.1–5).

Geographic and stratigraphic provenance. The holotype was found at Cabeza Blanca, Escalante Departament, and MLP 59-II-26-97 at Laguna de Los Machos, Paso de Indios Departament, Chubut Province, Argentina (Fig. 1). Both specimens come from late Oligocene levels of the Sarmiento Formation (Simpson, 1941), and both localities are regarded as Deseadan in age. A diverse and rich Deseadan fauna has been found in Cabeza Blanca (Loomis, 1914; Marshall *et al.*, 1983; Reguero and Escribano, 1996). Laguna de Los Machos yielded a less diverse fauna (Patterson and Pascual, 1968, p. 7; Patterson and Marshall, 1978, p.42) coming from light-colored tuff levels outcropping in the property of Mr. Belisario Escobar (currently belonging to EDELIN S.A.).

DESCRIPTION

Mandible. *Asteromys punctus* is the smallest known “eocardiid”. The mandibular body of the holotype is broken and deformed (Fig. 2.1–2). Thus, the new specimen MLP 59-II-26-97 (Fig. 3) provides new information on the mandibular anatomy of *A. punctus*. In labial view, MLP 59-II-26-97 (Fig. 3.1) has the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* (nMpi) between p4 and m1. This notch is united to the masseteric crest, forming a well-developed ridge that does not project laterally with respect to the lateral surface of the horizontal ramus. The horizontal crest is a low and broad ridge as in *Chubutomys leucoreios* Pérez, Vucetich and Kramarz, 2010. The lateral crest (Woods, 1972) is dorsally convex, although less than in other “eocardiids” (e.g., *Luantus*, *Chubutomys*, *Schistomys*), and dif-

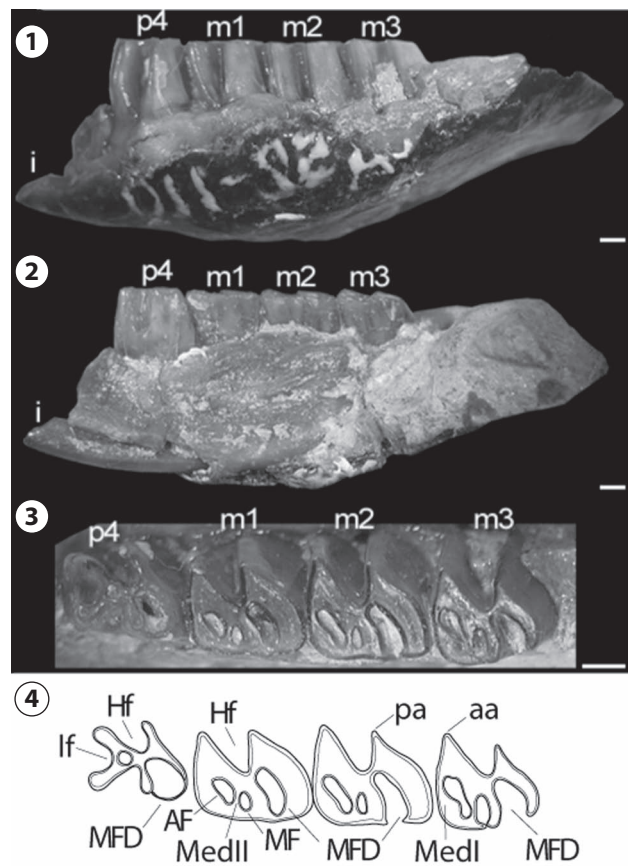


Figure 2. *Asteromys punctus*, holotype MACN-A 52-110. **1**, labial view; **2**, lingual view; **3**, occlusal view; **4**, dental nomenclature/nomenclatura dental. **Abbreviations:** aa, anterior apex; AF, anterofossettid; i, incisor; Hf, hypoflexid; If, longitudinal furrow; Med I, metalophulid I; Med II, metalophulid II; MF, mesoflexid or mesofossettid; MFD, metaflexid or metafossettid; p4, premolar; m1–m3, lower molars. Scale bar= 1 mm/ *Holotipo* MACN-A 52-110. **1**, vista labial, **2**, vista lingual, **3**, vista oclusal. **Abreviaturas:** aa, ápice anterior; AF, anterofosétida; i, incisivo; Hf, hipofléxido; If, surco longitudinal; Med I, metalofúlido I; Med II, metalofúlido II; MF, mesofléxido o mesofosétida; MFD, metafléxido o metafosétida; p4, premolar; m1–m3, molares inferiores. Escalas= 1 mm.

fering from other cavioids that have a straight lateral crest (e.g., *Dasyprocta*, *Dolichotis*). The coronoid process rises behind the m3 as in *Schistomys* and *Dolichotis*, whereas in *Dasyprocta* it rises behind the m2. The diastema is short and the mental foramen is close to the dorsal margin of the dentary and opens dorsolaterally as in *C. leucoreios* or *Luantus propheticus* Ameghino, 1898. The symphysis rises sharply and the posteroven-tral projection of the posterior end of the mandibular symphy-sis (“chin”) is only moderately developed, bearing a low bulge that projects ventrally. Lingually, in MLP 59-II-26-97 (Fig. 3.2) the mandibular foramen is below the dental series, at the level of the m3 crown as in other Caviioidea s.s. (e.g., *Dolicho-tis*, *Hydrochoerus*, *Cavia*, *Luantus*). The hystricognath fossa is shallower than in *Dasyprocta* but deeper than in *Phanomys*, *Schistomys*, and *Dolichotis*.

Lower teeth. The incisor is slender, with enamel on its anterior and lateral faces, and extends up to the posterior part of m2 as in the holotypes of *A. punctus*, *Chubutomys leucoreios*, and *Luantus propheticus*.

The cheek teeth of *A. punctus* are mesodont and the crowns are slightly lower than those of *L. initialis* (Tab. 1). Although the teeth of the holotype are slightly more worn, both specimens are interpreted as juvenile individuals. In this stage of wear, the enamel completely surrounds the crown of the cheek teeth. The hypoflexid is triangular, with rounded apex

and consistently located opposite to the metaflexid/metafos-settid, extending transversely up to half of the occlusal surface, and lacks cement (Figs. 2–3).

In MLP 59-II-26-97, the deciduous premolar was re-moved from the mandible, without damaging its roots nor the definitive p4. The morphology of this dp4 (Fig. 3.4–3.5) is similar to that of *Luantus propheticus* (e.g., MACN-SC 2076), but smaller in size. It is markedly worn, low-crowned, with two roots. This tooth is elliptical with the trigonid narrower than the talonid. In the anterior part, there is a small and sub-circular fossettid that could correspond to the anterofossettid. In the posterior portion, there is one long and narrow fosset-tid (metafossettid?) split in two smaller fossettids. A wide and shallow fossettid present on the labial side could be a hypofos-settid. The enamel completely surrounds the crown.

The p4 (Figs. 2–3) is typical of this taxon, because it is the only “eocardiid” with a non-molarized lower premolar, or at least not completely molarized, although it has a bilobed shape. On the anterior side, there is a wide and deep longi-tudinal furrow that becomes narrower toward the base of the crown; in occlusal view it is semicircular. The presence of this furrow is considered a primitive feature of caviomorphs (Vucetich and Ribeiro, 2003). The apex of the anterior lobe is sharp, elongate, and directed anteriorly.

In occlusal view, the holotype has a small fossettid in the

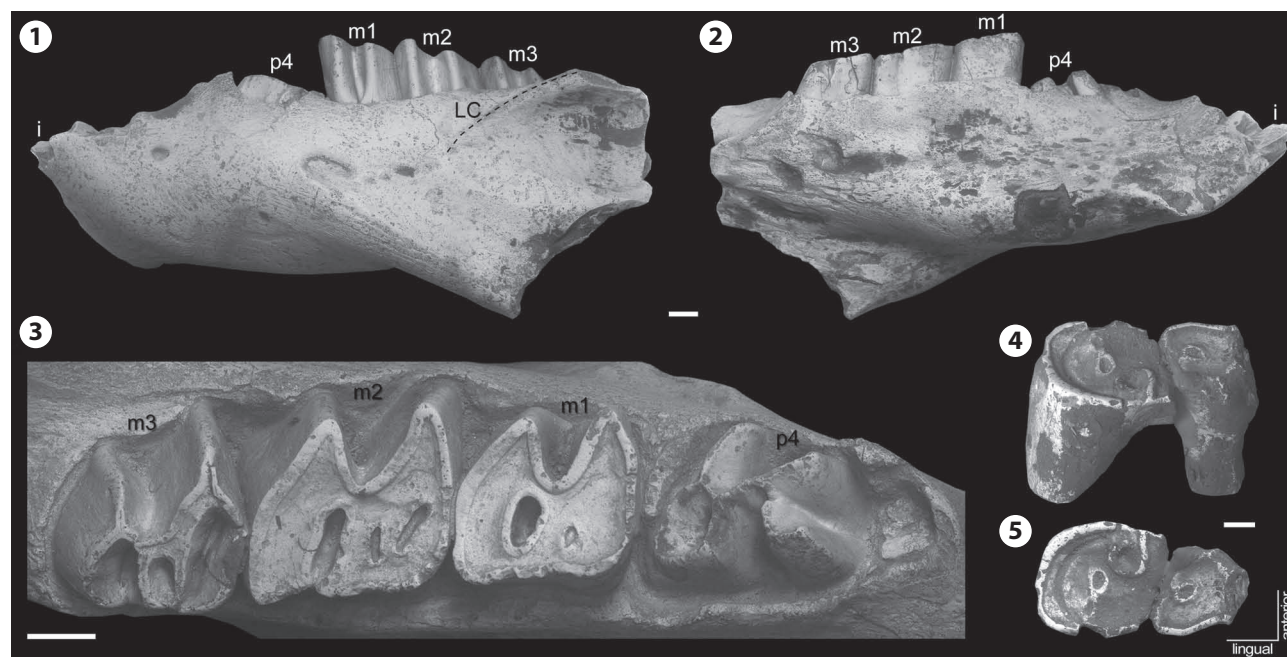


Figure 3. *Asteromys punctus*, MLP 59-II-26-97. **1**, labial view; **2**, lingual view; **3**, occlusal view; **4**, dp4 in lateral view; **5**, dp4 in occlusal view. Dashed line highlights the lateral crest. **Abbreviations:** i, incisor; LC, lateral crest; p4, premolar; m1–m3, lower molars. Scale = 1 mm. **Asteromys punctus**, MLP 59-II-26-97. **1**, vista labial; **2**, vista lingual; **3**, vista oclusal; **4**, dp4 en vista lateral; **5**, dp4 en vista oclusal. La cresta lateral se indica con línea de guiones. **Abreviaturas:** i, incisivo; LC, cresta lateral; p4, premolar; m1–m3, molares inferiores. Escalas = 1 mm.

middle of the p4, on the internal side of the ectolophid (Fig. 2.3–4); whereas MLP 59-II-26-97 has a shallow vertical furrow on the internal corner formed by the posterior wall of the first lobe and the ectolophid, which would correspond in topology to the small subcircular fossettid of the holotype (Fig. 3.3). Thus, this character may be different, independently from the stage of wear. The hypoflexid is very wide with a rounded apex and located opposite to the metaflexid. The posterior lobe is triangular, with a very large, elongate and deep metafossettid; the lingual apex is narrow and elongate. The hypolophid is long and joins the posterolophid forming the metafossettid (Figs. 2.3–4, 3.3). Lingually, both specimens have a wide and deep mesoflexid that reaches half of the crown (Figs. 2.2–4, 3.2–3). As Wood and Patterson (1959) pointed out, the holotype has a conical p4 in lateral view, and the upper part of the m1 curves anteriorly overlapping obliquely the upper part of the posterior side of the premolar (Fig. 3.1–2).

Molars are bilobed, with the lingual wall straight. They have wide, elongate, and persistent fossettids.

The lobes of m1 (Figs. 2.3–4, 3.3) are approximately equal

in size; the anterior and posterior walls of the anterior lobe are almost straight; the posterior lobe has the anterior wall straight but the posterior one is convex. In the holotype, the anterior lobe has two fossettids, the anterofossettid is elongate and antero-lingually oblique, in the middle of the lobe (Fig. 2.3–4). The mesofossettid is more posterior, smaller, and transversely elongate in both specimens; a wide and very elongate metafossettid is present in the posterior lobe, opposite the hypoflexid. In MLP 59-II-26-97, although dp4 was still attached to the dentary and p4 was just erupting, the anterofossettid of m1 has already disappeared, suggesting that the mesofossettid, although smaller, is more persistent.

In both known specimens, the m2 is similar in shape to the m1, but slightly larger; the posterior wall of the posterior lobe is slightly concave on the labial side and convex on the posterior part. There are two fossettids on the anterior lobe (Figs. 2.3–4, 3.3), the anterofossettid is elongate and antero-lingually oblique, located in the middle of the lobe, and the mesofossettid is smaller and transversely elongate. On the posterior lobe, the metaflexid, which is very elongate and opposite to the hypoflexid, is still open.

In MLP 59-II-26-97 (Fig. 3.3), the m3 is slightly smaller than the m1. Since it has little wear, the lingual apex of the anterior lobe is narrow and long and the apex of the posterior lobe is even longer; the anterofossettid and the mesofossettid are large, but the anterofossettid is wider; the posterior lobe is smaller, with its anterior wall slightly concave and the posterior convex; the metaflexid occupies almost the entire lobe. In contrast, in the holotype (Fig. 2.3–4), which is more worn, the m1–m3 are similar in size; the anterior lobe has the anterior wall slightly convex, the posterior wall is straight, and the apices of both lobes are not as conspicuous as in MLP 59-II-26-97. In the holotype the metalophid I widens at its lingual corner. This condition is not seen in MLP 59-II-26-97, probably because of its early stage of wear. In the holotype, the mesofossettid is large and deeper than the anterofossettid, and the metaflexid is very large, opposite to the hypoflexid.

In MLP 59-II-26-97 the p4 and m3 are less worn than in the holotype, whereas the m1–m2 are more worn. Although new findings are necessary to attain a more comprehensive knowledge about the ontogeny of *A. punctus*, differences between both specimens seem to be the result of intraspecific variation.

DISCUSSION

Phylogenetic position of Asteromys punctus

Character evidence. A recent cladistic analysis based on mor-

TABLE I - Dental measurements in millimeters/ Medidas dentarias en milímetros

		APL	AW	PW	H
Asteromys punctus					
MACNA 52-110 (Holotype)	<i>i</i>	2,6	1,7	2,0	
	<i>p4</i>	2,6	1,7	2,0	
	<i>m1</i>	2,8	2,3	2,3	1,21
	<i>m2</i>	3,0	2,5	2,5	
	<i>m3</i>	2,6	2,4	2,0	
MLP 59-II-26-97	<i>dp4</i>	3,6	1,4	1,9	
	<i>p4</i>	2,4	1,4	2,2	
	<i>m1</i>	2,6	2,3	2,2	
	<i>m2</i>	2,9	2,7	2,5	
	<i>m3</i>	2,2	2,3	1,9	
Luanthus initialis					
MACNA 52-164 (Lectotype)	<i>p4</i>	4,1	2,7	3,0	
	<i>m1</i>	5,0	3,9	4,1	1,28
	<i>m2</i>	5,7	4,6	4,6	

Abbreviations/ abreviaturas: APL, anteroposterior length/longitud antero-posterior; AW, anterior width/ ancho transverso anterior; PW, posterior width/ancho transverso posterior; H, crown height/altura de la corona.

phological characters, taking into consideration both known specimens of *A. punctus* and an extensive taxon sampling of basal Caviioidea *s.s.*, depicted *A. punctus* as the most basal taxon of Caviioidea *s.s.* (Pérez and Vucetich, 2011). Here we discuss the character-evidence supporting such results (Fig. 4) and the robustness of the arrangement of basal forms of Caviioidea *s.s.* using the Bremer index (Bremer, 1994).

The inclusion of *A. punctus* within Caviioidea *s.s.* is supported by the presence of four unambiguous synapomorphies: mandibular foramen below the m3, posterior extension of the root of the lower incisors extending up to the level of the posterior lobe of m2, lateral crest dorsally convex and deflecting anteroventrally from the base of the coronoid process, and horizontal crest with a low and broad ridge (Pérez and Vucetich, 2011). Additionally, the clade formed by Caviioidea *s.s.* is supported by eight ambiguous synapomorphies, seven of which are unknown in *A. punctus* (and other basal cavioids), and therefore these characters may represent synapomorphies

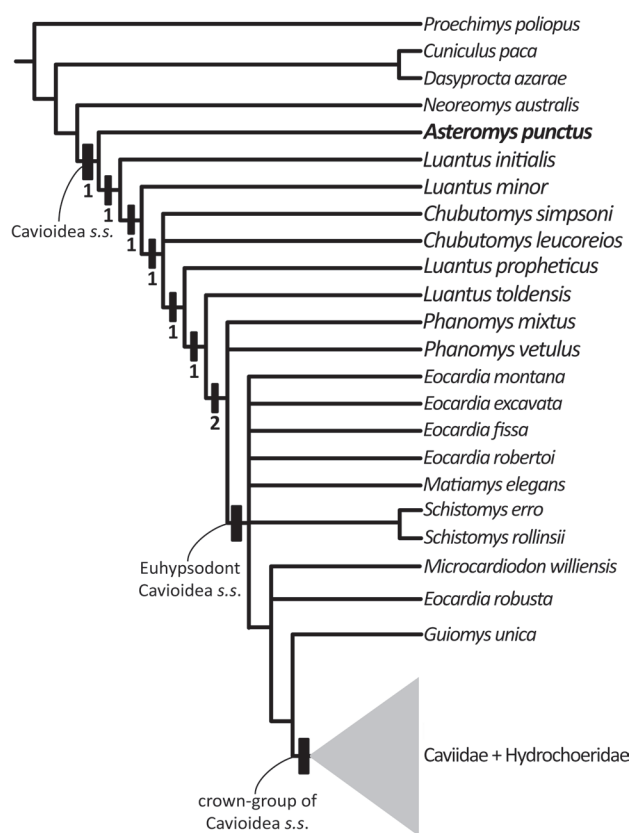


Figure 4. Summarized phylogenetic tree of Caviioidea *s.s.* based on the phylogenetic analysis of Pérez and Vucetich (2011). Crown-group of Caviioidea *s.s.* is collapsed into a single clade. The numbers in gray indicate the Bremer support values/ *Árbol filogenético reducido de Caviioidea s.s. sobre la base del análisis filogenético de Pérez y Vucetich (2011). El grupo corona de Caviioidea s.s. está colapsado en un único clado. Los números en gris indican los valores de soporte de Bremer.*

of Caviioidea *s.s.* or of less inclusive clades within this group. However, one of the eight ambiguous synapomorphies: depth of the fossa dorsal to the horizontal crest with respect to the dorsoventral depth of the nMpi is ambiguous because *A. punctus* shares with euhypsodont Caviioidea *s.s.* (except for caviines) a derived condition (fossa equal in depth to notch). More information of other basal cavioids (*e.g.*, *Luantus minor* Pérez, Vucetich and Kramarz, 2010, *L. propheticus*, *L. initialis*) are needed to determine whether this condition was convergently acquired in the terminal lineage leading to *A. punctus* and in derived forms or if it represents a synapomorphy of Caviioidea that was subsequently reversed in Hydrochoeridae (*i.e.*, *Cardiomys*, *Kerodon*, *Phugatherium*, *Hydrochoerus*) and Dolichotinae.

The basal position of *A. punctus* among Caviioidea *s.s.* is justified by the absence in this taxon of a single derived feature of the clade formed by *L. initialis* and more derived cavioids: presence of a constriction of the apex in each lobe of the molars (optimized as an unambiguous synapomorphy). Similarly, the node of *L. minor* and more derived cavioids is supported by a single unambiguous synapomorphy: protohypsodont, rooted with anteroposterior length of occlusal surface less than half the crown height. Both *A. punctus* and *L. initialis* have the plesiomorphic condition for this character: mesodont, rooted, with the anteroposterior length of occlusal surface approximately equal to crown height (Pérez and Vucetich, 2011).

Evolutionary interpretations. The Deseadan age of *Asteromys punctus* and its phylogenetic placement as the most basal member of Caviioidea *s.s.* provide key information for understanding the early evolution of this group. Although some authors (Wood and Patterson, 1959; Patterson and Wood, 1982; Kramarz, 2006) agreed on the cavioid affinities of *A. punctus*, they have disagreed in the position of this taxon in the different evolutionary scenarios proposed for Caviioidea *s.s.* We review here the evolutionary implications of the above described phylogenetic results, and contrast them with pre-cladistic evolutionary hypotheses proposed for the early evolution of Caviioidea *s.s.*

Two major evolutionary scenarios have been proposed for the early diversification of Caviioidea *s.s.* Wood and Patterson (1959) proposed the presence of an early split of the group into two distinct evolutionary lineages, one composed by *Asteromys* and *Luantus*, and other composed by *Chubutomys*, *Phanomys*, and euhypsodont cavioids (*Schistomys* and *Eocardia*). Kramarz (2006) also recognized an early evolutionary split that divided Caviioidea into two major evolutionary lineages. This author interpreted *Asteromys*, *Luantus*, and *Phanomys* as representing

an evolutionary series of increasing hypsodonty and related characters that leads to the euhipodont dental pattern of *Eocardia*. In addition, Kramarz (2006, p. 776) considered a second evolutionary lineage with *Chubutomys* as the early hypsodont radiation of the family derived from an “*Asteromys*-like ancestor” lacking direct relationships with later “eocardiids”.

The phylogenetic results discussed here depict protohypodont “eocardiids” (including *Chubutomys*) as successive outgroups of a clade formed by *Phanomys* and euhipodont cavioids, including derived “eocardiids” (e.g., *Eocardia*, *Schistomys*) and the crown-group cavioids (Fig. 4; see also Pérez and Vucetich, 2011). Consequently, the phylogenetic results contradict the idea of a basal split of Caviioidea *s.s.* into two distinct evolutionary lineages, as proposed by Wood and Patterson (1959) and Kramarz (2006). The basal position of *Asteromys* within Caviioidea *s.s.* implies that this taxon is the earliest off-shoot of a single evolutionary lineage leading to euhipodont cavioids. Thus, *Asteromys* should not be considered as belonging to a distinct lineage (“phyletic line”) together with *Luantus*, as proposed by Patterson and Wood (1959). Moreover, the evolutionary scenario proposed by Kramarz (2006) can be phylogenetically interpreted in two alternative ways depending on the meaning of “an *Asteromys*-like ancestor” (see above). One of them is that *Chubutomys* is the sister group of a clade composed by *Asteromys* and all other Caviioidea *s.s.*, and the other is that *Asteromys* is the sister group of *Chubutomys* and all other Caviioidea *s.s.* Notwithstanding the two interpretations, the key difference between the evolutionary scenario proposed by Kramarz (2006) and the phylogenetic analysis discussed here is that the former considers *Chubutomys* as one of the two basalmost forms of Caviioidea *s.s.* whereas the latter considers *Chubutomys* more derived than some species of *Luantus* (Fig. 4).

Although Bremer support values for all basal nodes of Caviioidea *s.s.* of the phylogenetic analysis are low (Fig. 4), phylogenetic hypotheses derived from the evolutionary scenarios previously proposed by Wood and Patterson (1959) and Kramarz (2006) are suboptimal under the parsimony criterion. Topologies compatible with the scenario proposed by Wood and Patterson (1959) are markedly suboptimal within the context of the dataset of the phylogenetic analysis discussed here and require nine extra steps. Thus, within the context of this phylogenetic analysis, the presence of two distinct evolutionary lineages during the early evolution of Caviioidea *s.s.* can be rejected based on the available character data.

On the other hand, the two topologies compatible with the scenario proposed by Kramarz (2006) are either moder-

ately suboptimal (two extra steps) when *Chubutomys* is placed as the sister group of *Asteromys* and all other Caviioidea *s.s.*, or markedly suboptimal (five extra steps) when *Asteromys* is placed as the sister group of *Chubutomys* and all other Caviioidea *s.s.* The character-evidence favouring the basal position of *Asteromys* and the much more derived position of *Chubutomys* in the phylogenetic analysis discussed here (Fig. 4) are found in the characters diagnosing the two successive nodes above *Asteromys* (see above). These transformations are the simplest to understand the earliest stages of cavioid *s.s.* evolution and diversification, which seems to be focused on the cheek teeth morphology. The key transformation recorded in the clade of *L. initialis*+Caviioidea *s.s.* is the acquisition of a constriction in the apex of molariforms. Subsequent evolutionary modifications are related to the evolution of hypsodonty, with a protohypodont condition acquired in the ancestor of *L. minor* and more derived cavioids.

CONCLUSIONS

Asteromys punctus, recorded in the Deseadan of Chubut (Argentina), is one of the earliest representatives of Caviioidea *s.s.*, and was previously known by a single mandibular fragment. The new specimen reported here, although incomplete, provides significant anatomical information of the mandibular dentition of this taxon that are relevant to properly diagnose this species and to justify its phylogenetic placement within Caviioidea *s.s.*

A. punctus has a unique combination of characters among South American Hystricognathi, such as (1) anteroposterior length of p4–m1 approximately equal to that of m2–m3; (2) p4 with a deep vertical furrow on the anterior face; (3) double heart-shaped occlusal surface, and mesodont molars; (4) cement absent; (5) very persistent fossettids.

The phylogenetic results discussed here suggest that a basal split of Caviioidea *s.s.* into two distinct evolutionary lineages—as suggested by previous authors—is unlikely. Instead, basal members of Caviioidea *s.s.* represent successive sister taxa of the clade formed by euhipodont cavioids, including the crown-group.

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