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Revision of the fossil rodent *Acaremys* Ameghino, 1887 (Hystricognathi, Octodontoidea, Acaremyidae) from the Miocene of Patagonia (Argentina) and the description of a new acaremyid

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Within South American rodents, the Acaremyidae is an independent fossil lineage of octodontoids represented in the late Oligocene–middle Miocene of Patagonia. *Acaremys* is represented by six species recorded in the early Miocene, which have not been re-studied since their original description. Morphological and phylogenetic analyses suggest that *Acaremys* is paraphyletic. Three species are valid, *Acaremys murinus*, *Acaremys major*, and *Acaremys messor*. *Acaremys karaikensis* is a junior synonym of *Acaremys murinus*. '*Acaremys*' *tricarinatus* is excluded from the genus being closely related to *Sciamys*. The new species, *Pseudoacaremys kramarzi*, is closely related to '*Acaremys*' *tricarinatus* and *Sciamys*. '*Acaremys*' *preminutus* is excluded from the family being closely related to the early Miocene *Protacaremys prior*, or living octodontoids. The phylogenetic analysis demonstrated that Acaremyidae includes *Platypittamys*, *Galileomys*, *Acaremys*, *Pseudoacaremys* and *Sciamys*. The new acaremyid increases the diversity of extinct octodontoids and added a new evolutionary lineage within Acaremyidae. The evolutionary history of the superfamily suggests that the hypsodonty and the consequently occlusal simplification evolved twice within Octodontoidea: in Acaremyidae and in Octodontidae. In addition, the cladistic analysis confirmed that most character ambiguities are due to missing data, and hence, it is essential to find better remains to elucidate the relationships among acaremyids.

Keywords: *Acaremys*; Octodontoidea; systematics; phylogeny; Santa Cruz Province; Miocene

1. Introduction

Octodontoidea is the most diverse superfamily of caviomorph rodents (those Hystricognathi endemic to South America) from a morphological, taxonomic and ecologic point of view (Reig 1989; McKenna and Bell 1997; Upham and Patterson 2012). They are recorded at least since the early Oligocene (Frailey and Campbell 2004; Vucetich et al. 2010) and became highly abundant and diverse since the early Miocene with at least more than 10 genera and almost 20 species, only in Patagonia. Recent studies have been focused on the clarification of general features of their evolution as well as on the relationships between the taxa of this clade (Arnal et al., *in press*; Verzi et al., *in press*). The results provided a refreshing vision about the evolution of the group. Despite these efforts, the relationships among species of genera from the interval Oligocene–middle Miocene were far less explored with phylogenetic methods.

Within Octodontoidea, Acaremyidae is an independent fossil lineage well represented in the late Oligocene–middle Miocene of Patagonia with no direct relationships with the living families (Vucetich and Kramarz 2003; Arnal and Pérez 2013; Vucetich et al., *in press*; but see Verzi et al., *in press*). Among acaremyids, *Acaremys* Ameghino, 1887 is considered one of the most specious lineages represented by six species. It is recorded in the Colhuehuapian and

Santacrucian ages (early Miocene Ameghino 1887, 1889, 1891, 1894; Scott, 1905; Bordas 1939; Vucetich and Kramarz 2003). *Acaremys murinus* was erected by Ameghino (1887) based on a group of specimens (syntype) including a partially preserved skull, a mandible and isolated teeth from the Santa Cruz River cliff (Santa Cruz Province, Argentina; Figure 1). Later, Ameghino recognised the species *Acaremys messor* (1889), *Acaremys karaikensis* (1891) and *Acaremys tricarinatus* (1894), all of them represented only by the type specimen. Scott (1905) recognised *Acaremys major*, and synonymised *Acaremys messor* and *Acaremys murinus*. Bordas (1939) erected the species *Acaremys preminutus* from the 'couches a *Colpodon*' of Patagonia (Bryn Gwyn, southern cliff of the Chubut River; Figure 1), which was the oldest species of the genus (Colhuehuapian age) so far known.

Acaremys has been traditionally related to the Santacrucian *Sciamys* Ameghino, 1887 forming the Acaremyidae Wood, 1949 (Acaremyinae *sensu* Ameghino, 1902). In a phylogenetic analysis, Vucetich and Kramarz (2003) validated Acaremyidae and delimited it to the genera *Acaremys*, *Sciamys* and *Galileomys* Vucetich and Kramarz, 2003. Later, Arnal and Pérez (2013) and Vucetich et al. (*in press*) obtained similar results using a modified version of the data matrix of Vucetich and Kramarz (2003).

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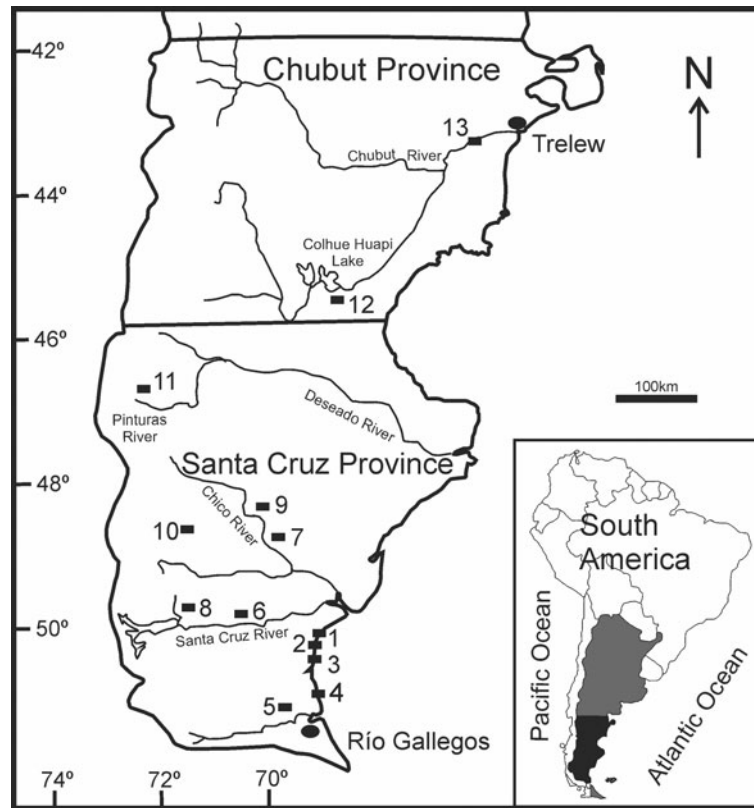


Figure 1. Map of the Santa Cruz and Chubut provinces (Argentinean Patagonia) showing the localities where *Acaemys* and *Pseudoacaremys* were found (1–8: Santacrucean localities; 9–11: Pinturan localities; 12 and 13: Colhuehuapian localities). 1, Monte León (Santacrucean Type locality); 2, La Cueva; 3, Monte Observación; 4, Corriegen Aike; 5, area of Estancia Killik Aike and Estancia Halliday; 6, area of the Santa Cruz River; 7, Estancia La Bajada; 8, Karaiken; 9, Gobernador Gregores; 10, Lago Cardiel; 11, area of the upper valley of the Pinturas River (including Los Toldos Sur); 12, Gran Barranca; 13, cliff of the Chubut River.

Nevertheless, the relationships of *Acaemys* vary within the family being the sister taxa of *Sciamys* (Vucetich and Kramarz 2003) or the earliest divergent acaremyid (Arnal and Pérez 2013).

The aim of this paper was to provide a new definition of the genus *Acaemys* with a revised diagnosis of the species traditionally included. This revision led to the recognition of a new genus and species of acaremyid, which improves the knowledge of Santacrucean octodontoids. In addition, we performed a phylogenetic analysis in order to study the relationships among these species and to corroborate the monophyly of the genus.

2. Materials and methods

We studied 45 specimens originally referred to *Acaemys*, 76 specimens referred to *Sciamys*, 15 specimens referred to *Galileomys*, 2 specimens referred to *Platypittamys*, as well as unpublished acaremyids represented by upper and lower teeth, mandibles and partially preserved skulls.

2.1 Anatomical nomenclature

Skull and mandibular nomenclature follows Wible et al. (2005). Tooth nomenclature follows Marivaux et al. (2004), Candela and Rasia (2012) and Vucetich and Ribeiro (2003) (Figure 2).

2.2 Cranial and mandibular abbreviations

ACH, anterior cranial height, measured at the snout in front of the premolar; ADW, anterior diastemal width, measured immediately behind the incisors alveoli; APW, anterior palatal width, measured at the level of P4/DP4; CW, cranial width; LDL, lower diastemal length; MBL, maximum bulla length; MBW, maximum bulla width; mc, masseteric crest; ment f, mental foramen; mf, mandibular masseteric fossa; MH1, anterior mandibular height, measured at the lowest point of the diastema; MH2, medial mandibular height, measured at the level of p4/dp4; MH3, posterior mandibular height, measured at the posterior border of m3; Mmmpio, medial masseteric muscle; ms, mandibular symphysis; PCH,

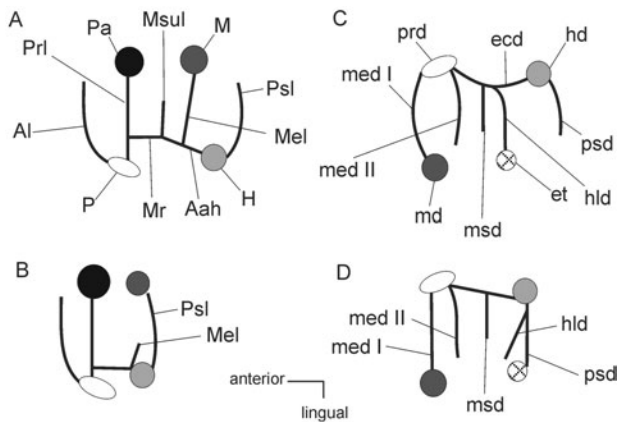


Figure 2. Dental nomenclature. (A) Upper molar and deciduous premolar; (B) upper permanent premolar: Aah, anterior arm of the hypocone; Al, anteroloph; H, hypocone; M, metacone; Mel, metaloph; Mr, mure; Msul, mesolophule; P, protocone; Pa, paracone; Prl, protoloph; Psl, posteroloph. (C) Lower molar and deciduous premolar; (D) lower permanent premolar: ecd, ectolophid; et, entoconid; hd, hypoconid; hld, hypolophid; md, metaconid; med I, metalophulid I; med II, metalophulid II; msd, mesolophid; prd, protoconid; psd, posterolophid.

posterior cranial height, measured at the squamosal; PDW, posterior diastemal width, measured immediately anterior to the ventral zygomatic root; PL, palatal length, measured from the posterior border of the incisors up to the mesopterygoid fossa; PPW, posterior palatal width, measured at the M3 hypoflex; SL, skull length, measured from the posterior border of incisors up to the occipital condyles; UDL, upper diastemal length.

2.3 Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; MACN A, Ameghino Collection, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MACN PV, Paleovertebrate Collection, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales de Mar del Plata, Mar del Plata, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Paleovertebrate Collection, Trelew, Argentina; YPM PU, Yale Peabody Museum, Princeton University, New Haven, USA.

2.4 Phylogenetic analysis

In order to assess the phylogenetic relationships of the species traditionally assigned to *Acaremys*, a cladistic analysis was performed. We used a modified version of the data-set of Arnal et al. (in press), which includes 37 taxa and 106 morphological characters; 5 taxa originally described as

Acaremys and 2 species of *Sciameys* were added. The late Oligocene *Deseadomys arambourgi* was deleted since it adds undesirable noise in the analysis. Eighteen multistate characters were considered additive (see Supplementary data 1). The data matrix was analysed using TNT 1.1 (Goloboff et al. 2008a, 2008b) followed by tree bisection reconnection (TBR) branch swapping algorithm (holding 10 trees per replicate). We used equally weighted parsimony to minimise the number of postulated evolutionary transformations. The robustness of the obtained MPTs was calculated with Bremer supports (relative and absolute frequencies). The character list and the data matrix are available as Supplementary data 1 and 2.

3. Systematic palaeontology

Order **RODENTIA** Bowdich, 1821

Suborder **HYSTRICOGNATHI** Wood and Patterson, 1955 (in Wood 1955)

Superfamily **OCTODONTOIDEA** Waterhouse, 1839

Family **ACAREMYIDAE** Wood, 1949

Genus *Acaremys* Ameghino, 1887

Horizon and locality. Trelew and Colhue Huapi Members of the Sarmiento Formation (early Miocene) (Spalletti and Mazzoni 1979; Bellosi 2010), Chubut Province, Argentina (Figure 1); Pinturas Formation (late early Miocene) (Bown and Larriestra 1990; Fleagle et al. 1995; Flynn and Swisher 1995), Santa Cruz Province, Argentina (Figure 1); Santa Cruz Formation (late early Miocene) (Marshall et al. 1983; Fleagle et al. 1995; Flynn and Swisher 1995), Santa Cruz Province, Argentina (Figure 1).

Emended diagnosis. Small- to medium-sized octodontoid. Teeth higher crowned than *Platypittamys* and lower crowned than *Sciameys*. Presence of unilateral hypsodonty, less evident than in *Sciameys*. Cusp individualised only in juvenile specimens. Parallel upper tooth rows, as in *Sciameys* and *Platypittamys*. Premolars normally replaced. Upper premolar with a poorly developed hypoflexus, unlike *Sciameys*, and absent or reduced metaloph. The lower premolar has a flexid separating protoconid and metaconid, deeper than in *Sciameys*. Lower molars with long posterolophid, unlike *Platypittamys* and *Galileomys*. Notch for the insertion of the Mmmppio conspicuous. The anterior portion of the mandibular masseteric fossa is deeper than in *Sciameys*. Masseteric fossa of the skull broad and limited anteriorly by an evident rim; nasals with a foramen of uncertain homologies located at the midpoint of the antero-posterior length of the bone; postorbital process well developed and presence of sagittal crest, unlike *Sciameys*.

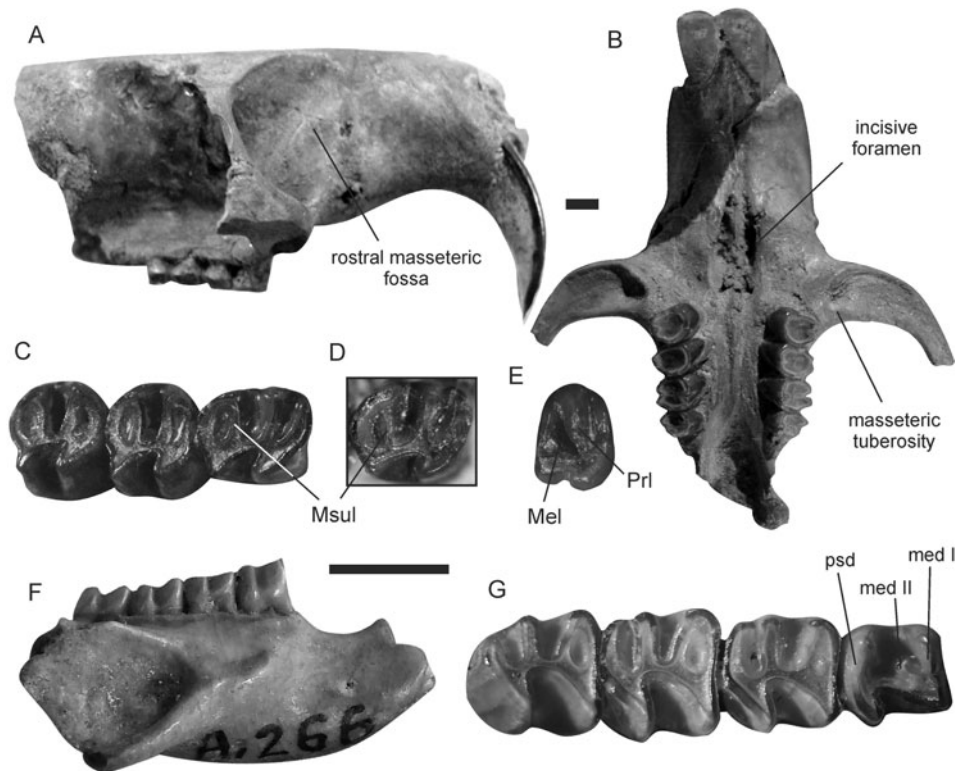


Figure 3. *Acaremys murinus*. AMNH 9280 skull with dentition (A) lateral view; (B) ventral view. (C) MACN A 10092, left DP4–M2 (reversed). (D) MLP 15-410 (Syntype), right DP4. (E) MACN A 4143, left P4 (reversed). MACN A 266 (Syntype) (F) lateral view of right mandible; (G) right p4–m3. Anterior to the right. Scale: 2 mm.

3.1 *Acaremys murinus* Ameghino, 1887

(Figure 3, Tables 1 and 2)

Acaremys karaikensis Ameghino, 1891: 249.

3.1.1 Syntype

MACN A 266, right mandible with p4–m3; MLP 15-410, anterior portion of the skull with right and left DP4–M1.

3.1.2 Type of the synonym

MACN A 1885, poorly preserved skull with right and left P4–M3.

3.1.3 Diagnosis

Size similar to '*Acaremys*' *tricarinatus*. Upper molars with parafossette and posterofossette delimited in juvenile

Table 1. Cranial and mandibular measurements of the species of *Acaremys* (cm).

	<i>Acaremys murinus</i>		<i>Acaremys major</i>	
	MACN A 1885	MACN A 10094	MMP 114M	YPM PU 15366
ACH	0.798	–		0.980
ADW	0.646	0.486		0.956
APW	0.346	0.318		
CW	–	1.000		
LDL			0.582	
MBL	–	–		
MBW	–	–		
MH1			0.458	
MH2			0.558	
MH3			0.344	
PDW	0.940	0.942		1.262
PPW	–	0.390		–
SL	–	–		6.420
UDL	1.332	1.146		1.698

Table 2. Dental measurements of the species of *Acaremys* (cm) and 'Acaremys'.

		APL	AW	PW
<i>Acaremys murinus</i>				
MACN A 266	p4–m3	7.34	–	–
	p4	1.68	1.44	1.70
	m1	1.82	1.88	1.98
	m2	1.98	2.24	2.02
	m3	1.86	1.98	1.68
MACN A 1885	P4–M3	7.24	–	–
	P4	1.76	2.28	2.18
	M1	1.78	2.32	2.26
	M2	1.98	2.44	2.20
	M3	1.72	2.26	1.86
MACN A 10092	DP4	2.30	2.02	1.96
	M1	1.92	2.26	2.16
	M2	1.98	2.24	2.28
MLP 15-410	DP4	2.28	1.82	1.82
	M1	1.70	1.90	1.90
MMP 114M	p4–m3	7.14	–	–
	p4	1.58	1.44	1.78
	m1	1.88	1.92	1.84
	m2	1.98	2.12	2.08
	m3	1.70	1.90	1.56
<i>Acaremys messor</i>				
MACN A 4106	dp4–m2	7.10	–	–
	dp4–m3	8.58	–	–
	dp4	2.65	1.43	1.63
	m1	2.25	1.92	1.95
	m2	2.20	2.01	1.84
	m3	1.48	1.52	1.36
' <i>Acaremys</i> ' <i>tricarinatus</i>				
MACN A 4113	p4–m3	8.10	–	–
	p4	1.96	1.64	1.80
	m1	2.06	2.06	2.00
	m2	2.08	2.16	1.98
	m3	2.00	1.92	1.52
MLP 15-24	P4–m2	5.90	–	–
	p4	1.62	1.44	1.94
	m1	2.04	1.98	1.92
	m2	2.04	2.02	1.98
MLP 84-III-8-43	p4–m3	7.72	–	–
	p4	1.92	1.58	1.84
	m1	1.90	2.06	1.96
	m2	2.02	2.24	2.12
	m3	1.96	2.02	1.56
' <i>Acaremys</i> ' <i>preminutus</i>				
MACN PV 11246	DP4–M2	5.30	–	–
	DP4	1.71	1.45	1.39
	M1	1.79	1.57	1.66
	M2	1.80	1.67	1.68

Notes: APL, anteroposterior length; AW, anterior width; PW, posterior width.

specimens. Simple p4, with well-developed metalophulid I, ectolophid and posterolophid, and variably developed metalophulid II. Skull with the furrow for the infraorbitalis nerve delimited by a well-developed lateral rim and the vertical ramus of the zygoma delicate, unlike *Sciamys principalis*.

3.1.4 Referred material

AMNH 9280, skull with all the dentition; MACN A 249, MACN A 4123, MACN A 4127, MACN A 4129, MMP 114M, left mandibles with p4–m3; MACN A 266 (Syntype), MACN A 1889, MACN A 1900, MACN A 4120, MACN A 4128, MACN A 4130, MACN A 4133, MACN A 12682, right mandibles with p4–m3; MACN A 1879, MACN PV SC1694, MACN PV SC2586, right mandibles with p4–m2; MACN A 1885, badly preserved skull with dentition; MACN A 4143, skull fragment with left P4–M1 and right M1–M3; MACN A 4246, left mandible with dp4–m1; MACN A 10091, right maxilla with P4–M1 and eight cheek teeth; MACN A 10092, anterior skull portion. dentition; MACN A 10094, skull with dentition; MACN PV SC1831, MACN PV SC2339, MACN PV SC2347, MACN PV SC2585 left mandibles with p4–m2; MACN PV SC2410, right mandible with m1–m2; MACN PV SC2587, maxilla with M1–M2; MACN PV SC2588 (in part), 36 isolated cheek teeth; MACN PV SC4046, right maxilla with P4–M2; MACN PV SC4047, two isolated molariforms; MACN PV SC4050, right mandible with m2; MACN PV SC4051, six isolated molariforms; MACN PV SC4078, right mandible with m1–m3; MACN PV SC4082, left mandible with m1–m3; MACN PV SC4099, left mandible with dp4; MLP 15-410 (Syntype), skull fragment with both DP4–M1; YPM PU 15895, anterior skull portion with right M2 or M3.

3.1.5 Horizon and locality

Sarmiento Formation, Colhué Huapi Member (early Miocene), Gran Barranca, Chubut Province (Figure 1) (MMP 114M); Pinturas Formation, upper sequence (late early Miocene), Los Toldos Sur (Pinturas valley) (MACN PV SC2585, SC2586, SC2587, SC2588), Gobernador Gregores (MACN PV SC4046, SC4047, SC4050, SC4051), Lago Cardiel (MACN PV SC4078, SC4082), Santa Cruz Province (Figure 1); Santa Cruz Formation (late early Miocene), Karaiken, (MACN A 1885, MACN PV SC4099); Santa Cruz River cliff (MACN A 249, 266, MLP 15-410), Corriegen Aike (MACN A 4143), Estancia Halliday (YPM PU 15895), Monte León (MACN PV SC2339, SC2347, SC2410), Monte Observación (MACN PV SC1694, SC1831), Yacimiento de Dipilus (MACN A 10094) all localities in Santa Cruz Province, Argentina (Figure 1).

3.1.6 Description

Skull. The nasals are wide anteriorly and tapering posteriorly, unlike *Sciamys principalis*, reaching the level of the dorsal root of the zygoma and the M1. The premaxillaries occupy the anterior half of the lateral wall of the snout (Figure 3(A)); the ascending processes of the premaxillaries occupy a large extension of the dorsal

portion of the rostrum ending posteriorly at the level of the premolar. The rostral masseteric fossa is large, similar to that present in *Sciomyx principalis*; it includes the incisor alveolus, and is mainly formed by the maxillary and secondarily by the premaxillary. This fossa is shallow and anteriorly limited by a rim that extends ventrally from the dorsal border of the rostrum, defining a blunt anterior limit of the fossa. Frontal bones are narrow anteriorly widening backward. The naso-premaxillary suture is strongly crenulated. A faint postorbital process is observed behind the orbit, followed by a small postorbital constriction. The dorsal root of the zygoma is at the level of the M1. The vertical ramus of the zygoma is delicate, unlike *Sciomyx principalis*, and antero-dorsally oblique (Figure 3(A)). The ventral root of the zygoma is in front of the P4 and its antero-posterior diameter is similar to the dorso-ventral diameter. In ventral view, the ventral root projects laterally and continues with the horizontal ramus of the zygoma. The masseteric tuberosity (for the insertion of the superficial masseter *sensu* Woods and Howland 1979) is rounded and well marked (Figure 3(B)). At the dorsal border of the ventral root of the zygomatic arch, there is a conspicuous rim that forms the external limit of the furrow for the passage of the infraorbitalis nerve.

The diastema is longer than the cheek tooth series (Tables 1 and 2; Figure 3(A),(B)). In lateral view, it is anteriorly concave and posteriorly flat, and higher than the interdental portion of the palate (Figure 3(A)). In ventral view, the diastema is very broad posteriorly, in front of the P4, as in *Sciomyx principalis* (Table 1; Figure 3(B)). The maxillary fossae are very deep in juvenile specimens and shallower in adults. The incisive foramina are broad, crossed by the premaxillary–maxillary suture at the middle of the antero-posterior length. They continue posteriorly with diastemal rims that extend up to the P4. The posterior palatine foramina are small and at the level of P4–M1. The maxillary–palatine suture is crenulated and V shaped, with the apex at the P4–M1. The posterior nares open at the M2–M3 (Figure 3(B)).

Upper teeth. The upper tooth series are almost parallel (Figure 3(B)) with the occlusal surface of P4–M3 slightly externally oriented owing to the unilateral hypsodonty. The teeth are quadrangular in outline, increasing their transverse diameter with wear (Table 2). Crests are narrower than flexi in juvenile specimens, but in adult they become wider. The P4 is smaller than M1 and M2 (Table 2).

The DP4 is tetralophodont, longer than wide (Table 2, Figure 3(C)). The anteroloph is long and anteriorly convex; its anterior wall shows a small depression close to the protocone. The protoloph is straight and anteriorly oblique; it is labially fused with the paracone. The right DP4 of MLP 15-410 (a specimen of the syntype) presents the third crest in position reduced (Figure 3(D)); this crest seems to correspond to the mesolophule because it is

disconnected from the metacone, being the fourth crest in position probably the fusion between metaloph and posteroloph. In specimens with little more worn DP4, the homologies of the third crest are not clear owing to the fusion of the crests (Figure 3(C)). The posteriormost crest is long, anteriorly concave and united labially to the metacone (Figure 3(C),(D)). The mesoflexus is the broadest and deepest flexus, being the paraflexus and the fusion of posteroflexus and metaflexus/fossette shallower. The hypoflexus is anteriorly oblique and little penetrating in the occlusal surface (Figure 3(C),(D)).

The P4 has three well-developed crests and a fourth, the metaloph, variably developed. The anteroloph is short, low and anteriorly convex. The protoloph is the longest crest and extends from the protocone to the conspicuous paracone (Figure 3(E)); it can be perpendicular to the antero-posterior axis of the tooth or posteriorly oblique. The metaloph is absent or reduced to a little crest fused to the posteroloph in juvenile specimens (Figure 3(E)). The protocone is more conspicuous and larger than the hypocone; both cusps are separated by a hypoflexus less developed than in *Sciomyx principalis*. Labial flexi are the most penetrating, being the mesoflexus the broadest and deepest.

The upper molars are tetralophodont. The occlusal surface is almost circular in juvenile specimens and widens with wear (Table 2). The curve anteroloph and the straight protoloph fuse labially delimiting a small and shallow anterofossette (Figure 3(C)). The mure is slightly oblique and extends from the postero-lingual border of the protoloph. The metaloph extends from the merging point of the mure with the anterior arm of the hypocone; it is straight and lingually fuses with the metacone (Figure 3(C)). The posteroloph is long and anteriorly concave; in juvenile specimens its labial end contacts the metaloph delimiting a shallow posterofossette (Figure 3(C)). Between the hypocone and the posteroloph there is a constriction that disappears with wear. In adult specimens, cheek teeth acquire a figure-eight occlusal morphology by the disappearance of the para and posterofossette (Figure 3(B)). The mesoflexus is the broadest labial flexus; it is straight and forms a mesofossette in senile specimens. The hypoflexus opposes the mesoflexus, and is less penetrating in the occlusal surface than the mesoflexus (Figure 3(C)); it is anteriorly oblique and the deepest in the crown. In adult and senile specimens it becomes transverse, disappearing only in senile specimens.

The upper incisors are laterally compressed. Their labial face is curve, and lingually forms a right angle. The enamel surface is thick and smooth. In lateral view, the wear surface is slightly curve. The base surpasses posteriorly the ventral root of the zygoma.

Mandible. The body of the mandible is sturdy. It is higher below the premolar and lowers posteriorly (Table 1). Anteriorly, the diastema is concave and shorter

than in *Sciamys principalis*. A large mental foramen is at the lowest point of the diastema (Figure 3(F)). The notch for the insertion of the Mmpio is deep, straight, horizontal and extends between p4 and m1. Ventrally, it is limited by an evident rim continuous with the masseteric crest (Figure 3(F)), which is postero-ventrally oriented. This crest is well developed and protrudes laterally from the mandible. The anterior portion of the masseteric fossa is very deep (Figure 3(F)), more than in the species of *Sciamys*. The furrow that limits antero-dorsally the masseteric fossa (lateral crest *sensu* Woods 1972) is shallow, and its anterior portion is ventrally limited by a rim that does not reach the base of the coronoid process (Figure 3(F)). This rim, the masseteric fossa, and the masseteric crest give a robust look to the mandible, distinctive of the genus. The coronoid process extends postero-laterally at the level of m2 or m2–m3 delimiting a broad retromolar fossa, lateral to the tooth row. The mandibular foramen is evident on the ascending ramus of the mandible between the base of the coronoid process and the mandibular condyle. On the lingual side of the mandible, the symphysis extends posteriorly up to the m1. Beneath the diastema, there is an evident ventral prominence. The mandible presents numerous accessory foramina. In ventral view, the hystricognath fossa is narrow.

Lower teeth. The m1–m3 have similar sizes, being the m2 a little larger (Table 2, Figure 3(G)). The dp4 has a posteriorly concave metalophulid I uniting protoconid and metaconid. The ectolophid extends from the posterior border of the protoconid. The mesolophid extends antero-lingually from the ectolophid and unites to the metaconid delimiting an anterofossettid. From the anterior border of the mesolophid, an antero-posterior crest divides the anterofossettid into a labial and a lingual fossettid, as in the species of *Sciamys*. The hypolophid is straight and merged lingually to the entoconid. In juvenile specimens, this crest is not fused to the anterior arm of the hypoconid. The posterolophid is anteriorly concave, and extends from the hypoconid to the lingual border of the tooth. The mesoflexid is the broadest, deepest and less penetrating of the lingual flexi; the posteroflexid is the most penetrating in the occlusal surface. The hypoflexid is deeper than the mesoflexid and posteriorly oblique.

The p4 is simple, as in *Platypittamys brachyodon* and *Galileomys antelucanus*. The metalophulid I connects the labio-lingually aligned protoconid and metaconid, unlike '*Acaremys*' *tricarinatus* and *Platypittamys brachyodon*. In juvenile and adult specimens, protoconid and metaconid are separated by an anterior flexid (Figure 3(G)). From the posterior border of the protoconid the ectolophid is posteriorly directed to the posterolophid. The metalophulid II is variably developed: anteriorly oblique defining an anterofossettid, postero-lingually oblique (Figure 3(G)) or reduced. The posterolophid is anteriorly concave and connects hypoconid and entoconid. In some specimens

(MACN A 266; MMP 114M), a little cusp is located at the antero-lingual border of the posterolophid.

The lower molars are tetralophodont and subrectangular, being the transverse diameter the longest (Table 2, Figure 3(G)). The metalophulid I is straight and unites protoconid and metaconid. From the protoconid extends a very oblique ectolophid. The metalophulid II extends far from the protoconid and joins the metaconid delimiting a straight and shallow anterofossettid (Figure 3(G)), unlike *Sciamys petisensis*. In MACN A 4246, this fossettid is divided by a posterior extension of the metalophulid I, as in *Platypittamys brachyodon* and some specimens of *G. antelucanus* and *Sciamys principalis*. The hypolophid and posterolophid disposition is as in the dp4. The posterolophid is long and anteriorly concave; the labial portion is almost straight and parallel to the anterior wall of the hypoflexid, whereas the lingual portion is curve and antero-labially oblique (Figure 3(G)). The meso-metaflexid is the broadest and deepest of the lingual flexi. The anterofossettid is worn away in juvenile adults and the posteroflexid disappears in senile specimens. The hypoflexid is the most penetrating flexid; in juveniles it is posteriorly oblique and in adults it becomes less penetrating and transverse. The occlusal surface is not totally simplified in senile specimens, unlike the species of *Sciamys*. As is usual in acaremyids and other octodontoids, m3 is smaller than m2 owing to the lingual position of the hypocone (Table 2).

The lower incisors are laterally compressed. As in the upper incisors, the enamel surface is smooth, and the anterior surface is labially curved and lingually forms a right angle. In lateral view, the wear surface is slightly curved. The tooth is long; extends below the tooth row and behind m3 curves labially ending near the coronoid process.

3.2 *Acaremys major* Scott, 1905

(Figure 4, Table 1)

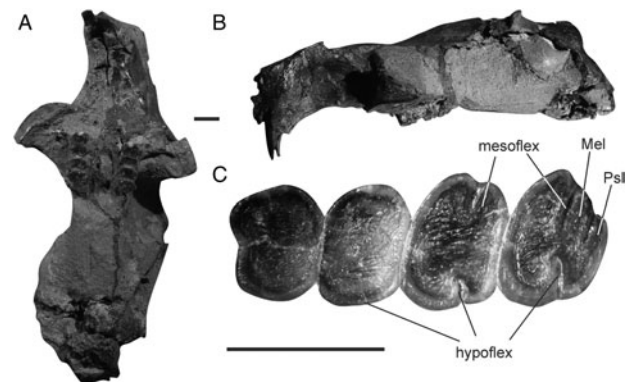


Figure 4. *Acaremys major* holotype YPM PU 15366, badly preserved skull with left and right cheek teeth. (A) Ventral view; (B) lateral view (reversed); (C) occlusal view of left P4–M3 (anterior to the left). Scale: 5 mm.

3.2.1 *Holotype*

YPM PU 15366, badly preserved skull with incisors, and left and right p4–m3.

3.2.2 *Diagnosis*

(Autapomorphies marked with asterisk) It is one of the largest fossil octodontoids, being 15% larger than *Acaremys murinus*. P4 and M1 are smaller than M2 and M3 in adult specimens, unlike other acaremyids in which M1 and M2 are the largest teeth. *M3 and M2 are similar in size. Labial shortening of the hypoloph and posteroloph on M3. Molariforms and incisors with a thin enamel layer, compared with other species of *Acaremys* and *Sciamys*. Skull with sagittal crest.

3.2.3 *Referred material*

Only the holotype.

3.2.4 *Horizon and locality*

Santa Cruz Formation (upper early Miocene), Killik Aike, Santa Cruz Province, Argentina (Figure 1).

3.2.5 *Description*

Skull. The skull is very long, with a robust rostrum (Table 1). The nasals occupy almost all the dorsal border of the snout, being wider anteriorly, as in *Acaremys murinus*. The premaxillaries are shorter than nasals, more than in *Acaremys murinus*. As in other acaremyids, the rostrum is posteriorly wider; nevertheless, its anterior portion is wide relative to *Acaremys murinus* and the species of *Sciamys* (Figure 4(A)). In lateral view, the diastema is concave (Figure 4(B)). The ventral root of the zygoma is located anteriorly to P4, and its antero-posterior length is similar to its dorso-ventral width. There is a smooth sagittal crest.

Upper teeth. Tooth rows are straight and parallel (Figure 4(A)), as in other acaremyids. The holotype is an adult-senile specimen with simplified occlusal surfaces (Figure 4(A),(C)). The P4 and the M1 are smaller than M2 and M3 in adult specimens, unlike other acaremyids. The P4 is totally simplified, M1 has a short hypoflexus and M2 has relicts of poorly penetrating mesoflexus and anteriorly oblique hypoflexus (Figure 4(C)). The posterior portion of the M3 is labio-lingually reduced by the shortening of the hypoloph and the posteroloph, unlike most octodontoids in which this decrease in size is due to the position of the hypocone labially placed with respect to the protocone (Figure 4(C)).

The upper incisors are similar to those of *Acaremys murinus*. They are laterally compressed with the smooth

enamel surface, labially curved and lingually forming a right angle. In lateral view, the wear surface is slightly curved (Figure 4(B)).

3.2.6 *Remarks*

This specimen was referred to *Acaremys* because of the presence of a sagittal crest, nasals wider anteriorly and the dental simplification (in adult specimens there are remains of structures on the occlusal surface). The use of the relative size to discriminate species is not a reliable tool when these differences are not conspicuous, as it is the case in most species of *Acaremys*. For example, since the original description of the species of *Acaremys*, several specimens were found which filled the gaps between size ranges of species (e.g. as was the case for *Acaremys murinus* and *Acaremys karaiensis*). Nevertheless, the size of the specimen referred to *Acaremys major* greatly exceeds that of the remaining acaremyids (Table 1). Therefore, there is no doubt of its assignment to a different *Acaremys* species.

3.3 *Acaremys messor Ameghino, 1889*

(Figure 5, Table 2)

3.3.1 *Holotype*

MACN A 4106, right mandible with dp4–m3.

3.3.2 *Diagnosis*

(Autapomorphies marked with asterisk) Size a little larger than in *Acaremys murinus*. Cheek teeth antero-posteriorly longer than labio-lingually wide, unlike the other species of *Acaremys*. The mandible has three mental foramina unlike other acaremyids, and the *notch for insertion of the Mmmpio at the middle of the mandible height.

3.3.3 *Referred material*

Only the holotype.

3.3.4 *Horizon and locality*

Santa Cruz Formation (upper early Miocene), Santa Cruz River cliffs, Santa Cruz Province (Figure 1).

3.3.5 *Description*

Mandible. The mandible of the only known specimen is broken anteriorly and posteriorly (Figure 5). The body of the mandible is sturdy as in the type species. Below the

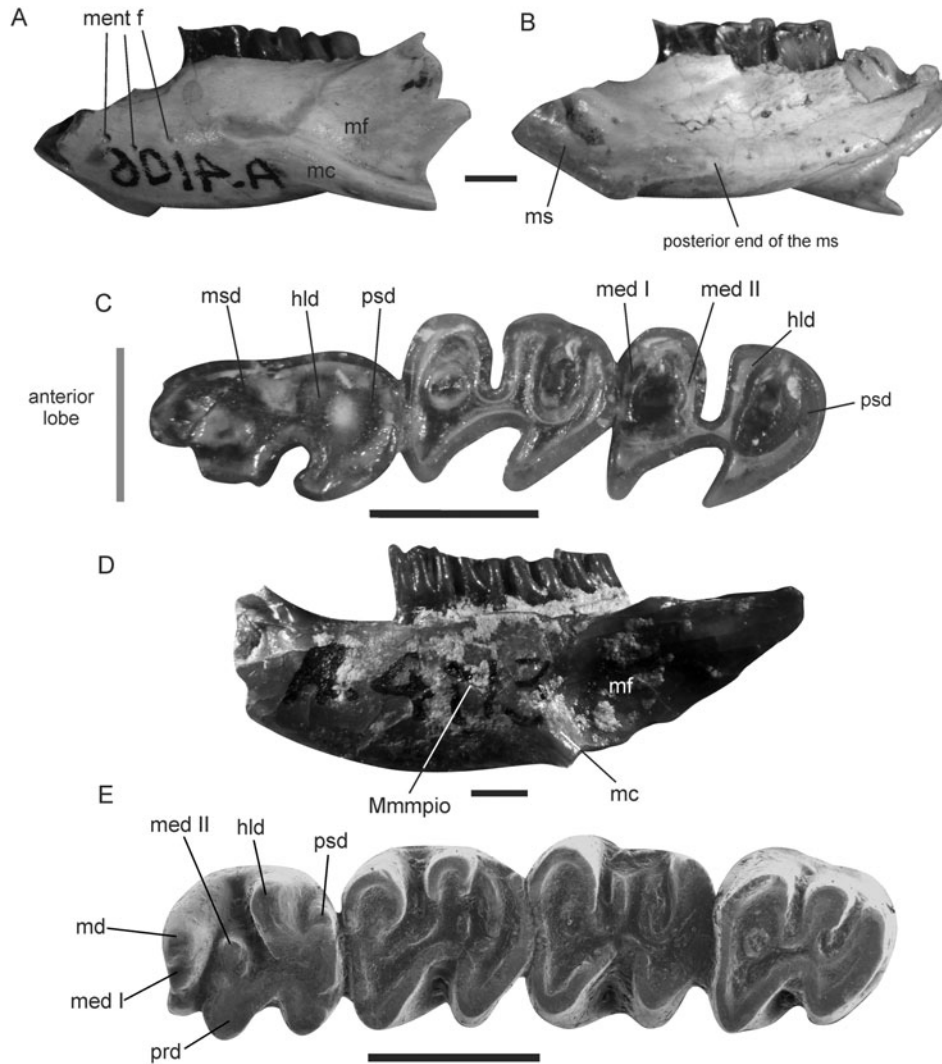


Figure 5. (A–C) *Acaremys messor* holotype MACN A 4106, right mandible with dp4–m3. (A) Lateral view (reversed); (B) lingual view (reversed); (C) right dp4–m2 (reversed). (D, E) '*Acaremys*' *tricarinatus* holotype MACN A 4113, right and left mandibles united at the symphysis, with right and left p4–m3. (D) Lateral view of the left mandible; (E) occlusal view of left p4–m3 and anterior to the left. Scale: 2 mm.

diastema there are three mental foramina, unlike the remaining species of the genus which have only one mental foramen, the anterior being the largest and the posterior being the smallest (Figure 5(A)). The notch for the insertion of the Mmmpio is very deep as in the type species; it extends below dp4–m1, and is a little oblique to the antero-posterior axis of the mandible. This notch lies at the middle of the mandible high, unlike the remaining species of *Acaremys* where it is above the mid high. Ventrally, it is limited by an evident rim as in the type species (Figure 5(A)). Posteriorly, this rim is continuous with a laterally extended masseteric crest. The anterior portion of the masseteric fossa is very deep, as in *Acaremys murinus*. The furrow that limits antero-dorsally the masseteric fossa is conspicuous, unlike *Acaremys murinus*, and is continuous with the insertion

of the Mmmpio (Figure 5(A)); its posterior end is at the level of the posterior portion of m2 and is continuous with the coronoid process. The coronoid process extends postero-laterally at the level of m2 delimiting a broad retromolar fossa, lateral to the tooth row.

On the lingual side of the mandible the symphysis is broad and extends posteriorly up to the m1 (Figure 5(B)). Beneath the posterior portion of the diastema is an evident ventral prominence (Figure 5(A),(B)). The mandible has numerous accessory foramina and seems to be dorso-ventrally compressed by post-mortem deformation.

Lower teeth. The m1–m3 are similar in size (Table 2, Figure 5(C)). The dp4 is deeply worn, but it seems to have the general acaremyid morphology: one anterior lobe and two posterior crests (Figure 5(C)). Based on the identification of primary homologies, we recognise the

anterior border of this lobe as the metalophulid I and its posterior border as the mesolophid. The two posterior crests correspond topologically to the hypolophid and posterolophid. The mesoflexid is posteriorly oblique and the deepest, since it is the only remaining flexid.

The lower molars are tetralophodont and their antero-posterior diameter is longer than the lateral one, unlike the other species of the genus (Table 2, Figure 5(C)). The general morphology of the molars is as in the type species. However, the anterofossettid of m2 has a particular shape: at the posterior wall of the metalophulid I and at the anterior wall of the metalophulid II there are two little spurs that give the anterofossettid an eight shape (Figure 5(C)). The m3 is just emerging from the alveolus and has no wear. It has the general tetralophodont pattern.

3.3.6 Remarks

Ameghino (1889) characterised *Acaremys messor* as the more robust species of the genus and provided some measurements. Nevertheless, the dental ones are not consistent with those taken by the authors, while the mandibular ones could not be measured because of the deformation of the type specimen.

3.4 ‘*Acaremys*’ *tricarinatus* Ameghino, 1894 (Figure 5, Table 2)

3.4.1 Holotype

MACN A 4113, right and left mandible united at the level of the symphysis with right and left p4–m3.

3.4.2 Diagnosis

(Autapomorphies marked with asterisk) Size similar to *Acaremys murinus*. Cheek teeth higher crowned than in the remaining species of *Acaremys*, as in the species of *Sciamys*; *p4 with a flexid separating the metalophulid I from the protoconid; metaconid anteriorly placed with respect to protoconid; hypolophid conspicuous and *posterolophid not connected to the entoconid, unlike the species of *Acaremys*; m1–m3 with the anterior lobe wider labio-lingually and antero-posteriorly shorter than the posterior lobe, unlike other acaremyids; *mandible without contact between the notch for insertion of the Mmmpio and masseteric crest, and anterior portion of the masseteric fossa shallower than in the remaining species of *Acaremys*, as in the species of *Sciamys*.

3.4.3 Referred material

MLP 15-24, left mandible with p4–m3; MLP 84-III-8-43, left mandible with p4–m2.

3.4.4 Horizon and locality

Santa Cruz Formation (upper early Miocene), Estancia La Bajada (MLP 84-III-8-43), Monte Observación (MACN A 4113) and Santa Cruz River cliff (MLP 15-24), Santa Cruz Province, Argentina (Figure 1).

3.4.5 Description

Mandible. The mandible has a long and poorly concave diastema, as in *Sciamys principalis* (Figure 5(D)). The mental foramen is located little posteriorly to the deepest point of the diastema. The notch for the insertion of the Mmmpio is well developed; it is deep, antero-posteriorly oriented below the p4–m1 (Figure 5(D)), as in *Acaremys murinus* and *Sciamys*. This notch is ventrally limited by a rim, as in *Acaremys murinus*. Posteriorly, the masseteric crest is not continuous with the notch in the holotype, as in *Galileomys eurygnathus* Kramarz, 2004, whereas in MLP 15-24 it is continuous. The masseteric fossa is shallower (Figure 5(D)) than in *Acaremys murinus* and the species of *Galileomys*. The furrow that limits antero-dorsally the masseteric fossa is poorly developed. The coronoid process extends laterally at the level of m3, delimiting a small and lateral retromolar fossa. A large mandibular foramen is placed dorsally to the base of the coronoid process.

Lower teeth. In the p4 the metalophulid I extends labially from the metaconid, and unlike other acaremyids it does not fuse with the protoconid, because both structures are separated by an anterior flexid (Figure 5(E)). This flexid is deep and converges with the anteroflexid isolating the metalophulid I from the remaining structures of the tooth (Figure 5(E)). The metaconid is more anterior than the protoconid. Two crests extend from the posterior border of the protoconid: a short metalophulid II posterolingually oblique and an ectolophid that extends posteriorly up to the posterolophid. From the posterior portion of the ectolophid extends a conspicuous hypolophid, similar to that present in *Sciamys*. The posterolophid does not reach the lingual border of the tooth in the holotype (Figure 5(E)), whereas in MLP 15-24 it does. The mesoflexid is the most penetrating and deepest lingual flexid; the anteroflexid and posteroflexid are equally deep, whereas the latter is poorly penetrating in the occlusal surface. The hypoflexid is the deepest one.

The m1–m3 have the anterior lobe wider than the posterior lobe, unlike other acaremyids (Table 2). The metalophulid I is straight joining the metaconid and protoconid, unlike the premolar (Figure 5(E)). A very oblique ectolophid extends from the posterior border of the protoconid. The metalophulid II is variably developed: in the holotype this crest is absent in m1 and reduced in m2–m3 (Figure 5(E)), whereas in MLP 15-24 it is complete on m1–m2. The metaconid and entoconid areas

are rounded, unlike *Acaremys murinus* and *Sciamys principalis*. The hypolophid extends from the union of the ectolophid and the anterior arm of the hypoconid; this crest is straight and reaches the lingual border of the teeth. The posterolophid is anteriorly concave and its lingual end lies close to the entoconid area, so it delimits a posterofossettid in adult specimens (Figure 5(E)). The anteroflexid merges with the mesoflexid in the m1 of the holotype, while in its m2 and m3 and in m1–m2 of MLP 15-24 there is a small anterofossettid (Figure 5(E)).

The lower incisors are laterally compressed, with the anterior smooth enameled surface, and formed a right linguall angle and a curve labial angle, as in *Acaremys murinus*. The incisors are long, and its posterior extreme is evident as a bulk at the external side of the mandible.

3.5 ‘*Acaremys*’ *preminutus* Bordas, 1939 (Figure 6, Table 2)

3.5.1 Holotype

MACN PV 11246 right maxillary fragment with DP4–M2.

3.5.2 Referred material

Only the holotype.

3.5.3 Emended diagnosis

(Autapomorphies marked with asterisk) Retention of the deciduous premolar unlike acaremyids. Upper cheek teeth longer than wide, unlike *Acaremys* and *Pseudoacaremys*. Upper cheek teeth with absence of figure-eight dental pattern, *crests anterolabially–posterolingually oblique and *anterolingual angle of M1–M3 forming a right angle as in *Protacaremys prior* and unlike acaremyids. M2 longer than wide * unlike acaremyids.

3.5.4 Horizon and locality

Sarmiento Formation, Trelew Member (early Miocene) (Simpson 1935; Mendía and Bayarsky 1981), South cliff of the Chubut River, Bryn Gwyn, Chubut Province, Argentina (Figure 1).

3.5.5 Description

Upper teeth. All upper cheek teeth are tetralophodont, and longer than wide (Figure 6, Table 2), unlike the species of *Acaremys*. They never acquire the typical acaremyid octodontoid dental pattern.

The most distinctive character is the retention of the deciduous premolar, unlike the remaining acaremyids. This tooth is more worn than the following teeth and has the general tetralophodont morphology of other fossil octodontoids (i.e. *Protacaremys*, *Prospaniomys* and *Acarechimys*). The crests are narrower than in the species of *Acaremys* and separated by wider and deeper flexi (Figure 6). The anteroloph is long and anteriorly convex; its anterior wall shows a small depression close to the protocone and near the base of the crown. The protoloph is straight and anteriorly oblique (Figure 6); it is labially fused with an enlarged area of the paracone. The labial end of anteroloph and protoloph is very close and would have fused with little more wear. The metaloph starts from the junction of the mure and the anterior arm of the hypocone extending up to the metacone. The posteroloph forms the posterior margin of the tooth and connects the hypocone and the metacone. Since early stages of wear, it is labially fused with the metaloph enclosing a posterior fossette (Figure 6).

The M1–M2 occlusal surface is almost quadrangular, little longer than wide (Table 2), unlike *Acaremys murinus*. The morphology of M1 and M2 is essentially as in the DP4, except for the presence of a right-angle anterolingual corner (Figure 6), as in *Protacaremys prior*.

3.5.6 Remarks

Bordas (1939) misinterpreted important features of the dentition of the holotype. Especially important, he mistook the first tooth of the series with a P4 when in fact it is a retained DP4. The retention of the DP4 through life is an essential trait of octodontoids, and is a characteristic of modern lineages. It apparently evolved several times independently, but its evolutionary importance has to be considered in a broad context.

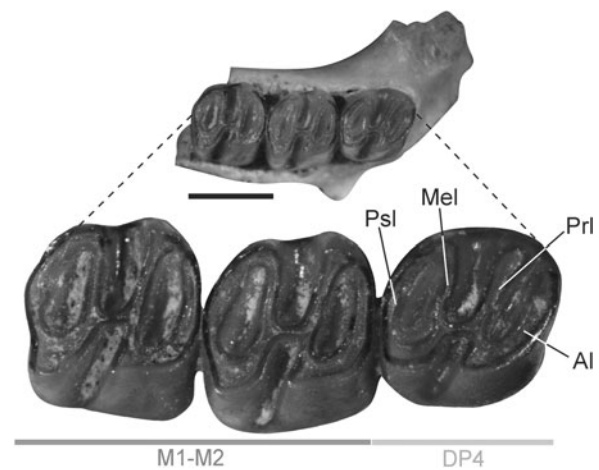


Figure 6. ‘*Acaremys*’ *preminutus* holotype MACN PV 11246, right maxilla with DP4–M2. Anterior to the right. Scale: 2 mm.

3.6 *Pseudoacaremys* n. gen.

Acaremys Ameghino 1887: 451 in part. Scott 1905: plate LXVII in part.

(Figure 7, Tables 3 and 4)

3.6.1 Type species

Pseudoacaremys kramarzi n. sp.

3.6.2 Derivatio nominis

From Greek pseudos (false) and *Acaremys* in reference to the erroneous original assignment of these materials to the genus *Acaremys*.

3.6.3 Diagnosis

(Autapomorphies marked with asterisk) Size similar to *Acaremys murinus*. Upper premolar trilophodont; the proto-loph with a very thin connection with the protocone, *hypocone labially placed with respect to the protocone and hypoflexus less developed than in *Acaremys murinus* and *G. antelucanus*. Upper molars with an accessory cusp in the proto-loph between protocone and paracone unlike *Acaremys*, *Galileomys*, *Sciomy*s and *Platypittamys*, and *hypocone labially placed with respect to the protocone; proto-loph of M3 with a thin connection to the protocone, as in P4. The molars are wider anteriorly than posteriorly, as in '*Acaremys*' *tricarinatus*. Skull *without a furrow for the

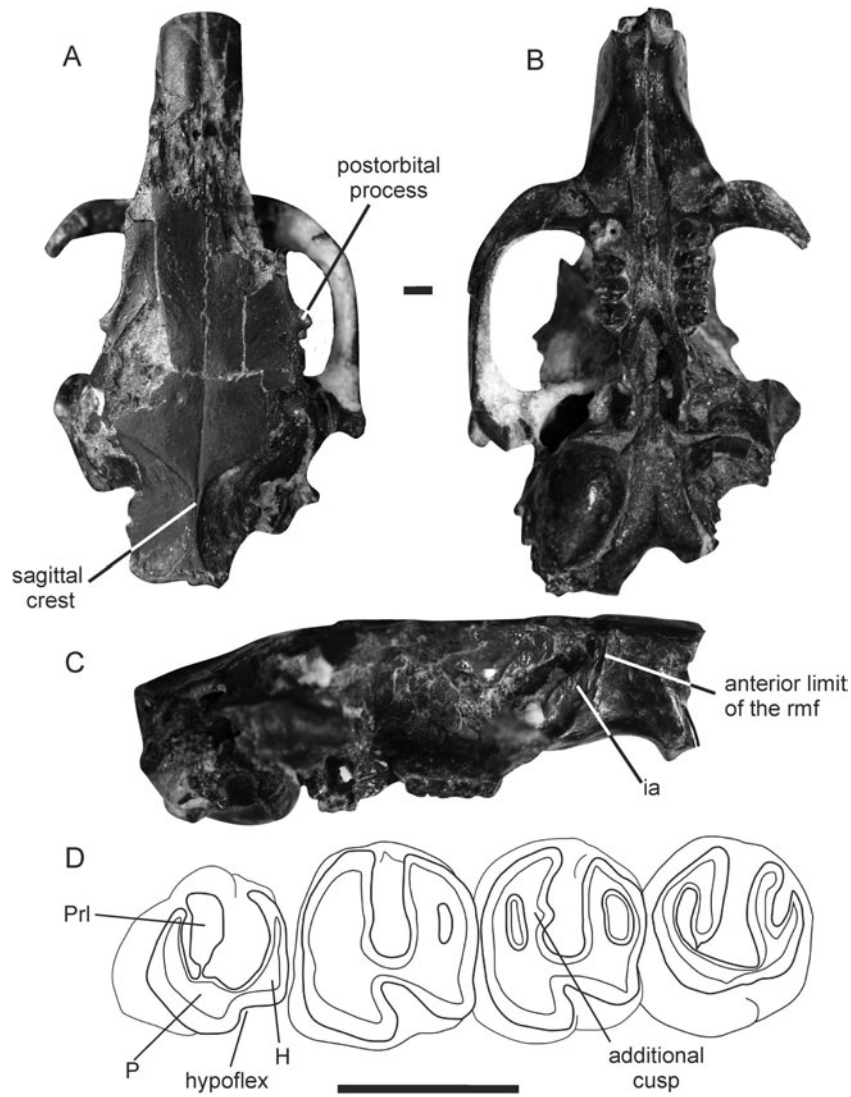


Figure 7. *Pseudoacaremys kramarzi*, holotype MACN A 10095, skull with dentition. (A) Dorsal view of the skull; (B) ventral view of the skull; (C) lateral view of the skull; (D) diagram of the left tooth row (P4–M3) anterior to the left. Scale: 2 mm.

Table 3. Cranial measurements of *Pseudoacaremys kramarzi* (cm).

	MACN A 10095
ADW	0.548
APW	0.366
CW	1.992
MBW	0.590
PDW	1.036
PPW	0.362
ACH	1.280
PCH	1.020
SL	4.060
UDL	1.456
MBL	1.057
PL	2.134

Table 4. Dental measurements of *Pseudoacaremys kramarzi* (mm).

		APL	AW	PW
MACN A 10095	P4–M3	7.27	–	–
	P4	1.55	2.20	1.68
	M1	1.96	2.40	2.26
	M2	1.94	2.28	2.20
	M3	1.82	2.22	1.42
MLP 15-197a	P4–M1	3.86	–	–
	P4	1.80	2.18	1.98
	M1	2.06	2.34	2.28

Notes: APL, anteroposterior length; AW, anterior width; PW, posterior width.

passage of the infraorbitalis nerve, *ventral root of the zygoma antero-posteriorly long and dorso-ventrally short, unlike other acaremyids and presence of a well-developed sagittal crest, unlike *Sciamys*.

3.6.4 *Pseudoacaremys kramarzi* n. sp.

Acaremys murinus Ameghino 1887: 451.

Acaremys murinus Scott 1905, plate LXVII.

3.6.5 *Derivatio nominis*

The specific epithet is in honour to Dr Alejandro Kramarz (MACN) for his studies on caviomorph rodents and for the valuable help given to one of the authors (MA).

3.6.6 *Diagnosis*

As for the genus.

3.6.7 *Referred material*

MACN A 10091, right isolated M1 or M2; MLP 15-197a, maxilla with P4–M1; YPM PU 15872, two maxillary remains with M1–M3.

3.6.8 *Horizon and locality*

Santa Cruz Formation (upper early Miocene), Santa Cruz River cliffs (MLP 15-197a), La Cueva (MACN A 10095)

and Killik Aike (YPM PU 15872), Santa Cruz Province (Figure 1).

3.6.9 *Description*

Skull. The description is based mainly on the holotype, an almost complete skull with no evidence on post-mortem deformation (Figure 7). The skull is long and low (Table 3), similar to *Sciamys principalis*. The anterior border of the nasals is blunt and they widen posteriorly, as in *Acaremys murinus* and unlike *Sciamys principalis*. Its posterior extension cannot be seen because they are broken (Figure 7(A)). The premaxillary–maxillary suture is very crenulated; its vertical part is posteriorly oblique in its ventral side, and it intersects the incisive foramina at the mid-point of its antero-posterior length (Figure 7(B)). The premaxillaries occupy the anterior half of the lateral wall of the snout. As in *Acaremys murinus* and *Sciamys principalis*, the rostral masseteric fossa is broad and mainly formed by the maxillary and secondarily by the premaxillary; it includes the incisor alveolus, and is anteriorly limited by a rim of the premaxillary that extends ventrally from the dorsal border of the rostrum (Figure 7(C)).

The frontals widen posteriorly, as in *Acaremys murinus*. An evident postorbital process and a little marked post-orbital constriction are present, unlike *Acaremys murinus* and *Sciamys principalis* (Figure 7(A)). The fronto-parietal suture is almost straight. The ventral root of the zygoma is anterior to the P4 and its antero-postero diameter is twice the dorso-ventral one, unlike other acaremyids; at its dorsal border, there is no rim delimiting the furrow for the passage of the infraorbitalis nerve, unlike other acaremyids. In ventral view, the ventral zygomatic root projects laterally forming an arch continuous with the horizontal ramus of the zygoma. The masseteric tuberosity is shallower than in *Acaremys murinus*. The depression for the insertion of the lateral masseteric muscle is shallow and extends posteriorly up to the maxillary–jugal suture. The dorsal root and the vertical ramus of the zygoma are not preserved. The horizontal ramus of the zygoma is high and formed mainly by the jugal. The paraorbital process is small, formed mainly by the jugal and by a small portion of the squamosal. The jugal–squamosal suture is antero-posteriorly long and oblique. The jugal fossa (for the origin of the posterior masseter muscle *sensu* Woods and Howland 1979) is shallow, antero-posteriorly long and high, occupying almost all the lateral face of the horizontal ramus. The squamosal forms the posterior zygomatic portion. The parietals reach the posterior border of the skull. Anteriorly they are vaulted, flattening to the back. There is a conspicuous sagittal crest (Figure 7(A)), unlike *Sciamys principalis*.

The auditory bulla is formed by the ectotympanic, as in extant rodents (Van der Klaauw 1931) (Figure 7(B)). It is small (Table 3), as in *Sciamys principalis*. The meatus

acusticus externus (MAE) is located at the antero-posterior centre of the bulla and is slightly dorsal to the midpoint of the dorso-ventral length; it is large, subcircular and antero-ventrally limited by a poorly extruding rim. Below the MAE, there is a conspicuous accessory foramen. The epitympanic and hypotympanic sinuses are not inflated. In ventral view the bulla is almost oval, wider anteriorly than posteriorly (Figure 7(B)). The antero-medial corner of the bulla exhibits a small prominence, and on the medial wall near the contact with the basioccipitals there is a small foramen of uncertain homologies. The occipital region is low and badly preserved.

In lateral view, the diastema is anteriorly concave and posteriorly plane, as in some specimens of *Acaremys murinus* and *Sciамys principalis*. In ventral view, the diastema is longer than the cheek teeth series (Table 3 and 4) and posteriorly wide, as in other acaremyids (Figure 7(B), Table 3). The incisive foramina are broad and posteriorly continue with the diastemal rims that extend up to the anterior portion of the interdental portion of the palate, as in *Acaremys murinus*. The maxillary fossae are shallow, unlike *Acaremys murinus*. The posterior palatine foramina are small and at the level of M1, unlike *Acaremys murinus*. They are separated by a poorly developed medial keel. The posterior nares open at the level of M3, delimiting a triangular mesopterygoid fossa (Figure 7(B)). Oval and conspicuous sphenopalatine vacuities are located at the level of the presphenoid and basisphenoid. The suture between basisphenoid and basioccipital cannot be distinguished. Posteriorly, on the basioccipitals and between both tympanic bulla there is an evident medial keel.

Upper teeth. The upper premolars are trilophodont (Figure 7(D)) and smaller than the molars (Table 4). The anteroloph is short and anteriorly convex, as in *Acaremys murinus*. The anterior wall of the anteroloph shows a small depression near the protocone, similar to *Platypittamys brachyodon*. The protoloph extends lingually from the paracone and its contact with the protocone is weak (Figure 7(D)). The hypocone is small and the hypoflexus is poorly developed (Figure 7(D)), less than in *Acaremys murinus* and *G. antelucanus*.

The upper molar morphology is similar to that of *Acaremys murinus*. Nevertheless, the protoloph has a conspicuous cusp in the protoloph, not present in other acaremyids (Figure 7(D)), and the hypocone is labially to the protocone. The mesoflexus is broader than in the other species of *Acaremys* and *Sciамys*. In M3 of MACNA 10095 and YPM PU 15872, the protoloph has a very thin union with the protocone, as in P4 (Figure 7(D)).

4. Phylogenetic analysis

The parsimony analysis resulted in 14 most parsimonious trees (MPTs) of 394 steps, with a consistency index (CI) of

0.368 and a retention index (RI) of 0.558, found in 133 out of the 1000 replicates. The strict consensus (Figure 8) corroborates that Acaremyidae is a monophyletic group including *Platypittamys*, *Galileomys*, *Acaremys murinus*, *Acaremys major*, *Acaremys messor*, ‘*Acaremys*’ *tricarinatus*, *Pseudoacaremys* and *Sciамys*. ‘*Acaremys*’ *preminutus* is excluded from the family (see below). Two synapomorphies support the monophyly of Acaremyidae: normal replacement of the deciduous premolars (character 5[0]) and hypocone buccal with respect to the protocone on M3 (character 45[0]). *Platypittamys brachyodon* is the basal most acaremyid and is excluded from the remaining acaremyids by the absence of four synapomorphies: figured-eight upper molars (character 28[1]), anteroloph reaching paracone on M1–M3 (character 31[1]), presence of an anterior flexid between protoconid and metaconid on p4 (character 64[0]) and a metalophulid II mesio-buccally connected to the metaconid (character 79[0]). *Galileomys antelucanus* is the next most divergent lineage (Figure 9). The remaining acaremyids are grouped in a clade characterised by eight synapomorphies: absence of terraced occlusal surfaces (character 6[1]), hypocone lingually aligned to protocone on P4 (character 23[1]), equal size of paracone and metacone on upper molars (character 32[1]), M1 longer than wide (character 50[1]), p4 equal in length and width (character 74[2]), ephemeral fossetids (character 75[1]), long posterolophid on lower molars (character 82[1]) and groove for the passage of the infraorbital nerve delimited by a large lateral rim (character 105[1]). The species originally referred to *Acaremys* are not grouped in a monophyletic clade. The relationships of *Acaremys murinus*, *Acaremys major* and *Acaremys messor* are not resolved, and form a polytomy in the strict consensus (Figure 8). Nevertheless, in the MPTs, the three taxa appeared as successive sister taxa of the clade including *Pseudoacaremys*, ‘*Acaremys*’ *tricarinatus* and the species of *Sciамys* (Figure 8). In all MPTs, *Acaremys major* is the earliest divergent lineage and in 13 MPTs *Acaremys messor* is the next divergent lineage being *Acaremys murinus* the sister taxa of the most derived clade (only in one MPT *Acaremys messor* is more closely related to the anteriorly mentioned clade). Nevertheless, these nodes are supported by zero-length branches (they have no character support). The study of the characters indicates that the lack of resolution is due to the presence of missing data in the fossil specimens and not to conflict between the characters. *Pseudoacaremys kramarzi* is the sister group of the clade formed by [‘*Acaremys*’ *tricarinatus* (*Sciамys principalis* + *Sciамys petisensis*)]; this clade is characterised by having protohypsodont cheek teeth (character 3[2]) and M1 and M2 similar in size (character 48[1]). The new species is characterised by having a hypocone labial to protocone on the upper cheek teeth, a ventral root of the zygomatic arch of which the anteroposterior diameter is twice the dorsoventral one and the absence of a groove for

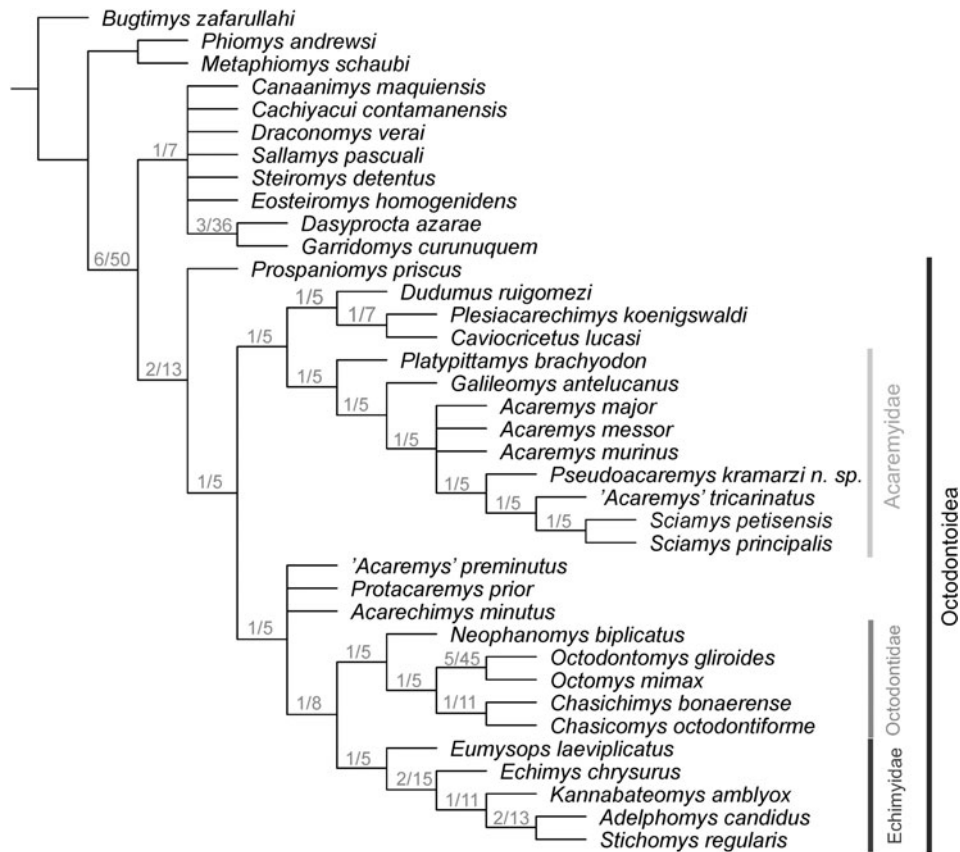


Figure 8. Strict consensus of the 14 MPTs (tree length = 394 steps; CI = 0.368 and RI = 0.558) resulting from a cladistic analysis of 37 taxa and 106 characters showing the relationships of the *Acaremys* species. Numbers above nodes separated by slash are absolute and relative Bremer support values.

the passage of the infraorbitalis nerve within the infraorbital foramen. The supports values of the nodes delimiting the family and nodes within it are relatively low (Figure 8).

The basal most divergent lineage within Octodontoidea is *Prospaniomys priscus* and the superfamily is characterised by the retention of the deciduous premolars (character 5[1]), absence of the anterior arm of the metacone on DP4 (character 10[0]), absence of mesolophule on upper molars (character 36[1]), metaloph lingually attached to the anterior arm of the hypocone on upper molars (character 38[0]), more lingually connected to the protoloph (character 43[1]), absence of the posterior arm of the metaconid on dp4 (character 53[0]) and lower incisors with an anterior right lingual border and a curved labial border (character 94[1]). The node defining Octodontoidea is relatively well supported (Figure 8).

'*Acaremys*' *preminutus* is excluded from the Acaremyidae. Based on this analysis, it is included in the clade leading to the living Octodontidae and Echimyidae (Figure 8). It forms a polytomy with the early Miocene *Protacaremys prior* and *Acarechimys minutus*. In 7 of the 14 most parsimony trees (MPTs) '*Acaremys*' *preminutus* is

closely related to *Protacaremys prior*, and in the remaining seven MPTs it is the sister taxa of Echimyidae + Octodontidae. This analysis also supports the monophyly of Octodontidae (including the late Miocene *Neophanomys biplicatus*, *Chasicomys octodontiforme* and *Chasichimys bonaerense* and the living *Octomys mimax* and *Octodontomys gliroides*) and Echimyidae (including the early Pliocene to early Pleistocene *Eumysops laeviplicatus*, the living *Echimys chrysurus* and *Kannabateomys amblyox* and the late early Miocene *Stichomys regularis* and *Adelphomys candidus*). The clades including living forms are the best-supported nodes of the superfamily (Figure 8).

5. Discussion and conclusions

5.1 Taxonomic status of *Acaremys*

Ameghino described the species of *Acaremys* without assigning materials or giving information of precise stratigraphic and geographic provenance. Moreover, some of the materials on which he based the morphological descriptions could not be identified (e.g. a skull of *Acaremys murinus* with P4–M3, a mandible of *Acaremys*

karaikensis) due to loss or breakage of fossil specimens (see Fernicola 2011, and discussion herein). Posteriorly, Scott (1905) and Bordas (1939) described two new species providing complete taxonomic information (see Section 1). The morphological review and the phylogenetic analysis carried out in this work suggest that only three of the six nominal species previously referred to *Acaremys* are valid. Two species are excluded from the genus (*'Acaremys' tricarinatus* and *'Acaremys' preminutus*) and a new species is described (*Pseudoacaremys kramarzi*).

Based on the phylogenetic results obtained in this work, the genus *Acaremys* including all the originally described species is paraphyletic (Figure 8). The type species, *Acaremys murinus*, is the most abundant in the fossil record and is represented by almost complete skulls and mandibles and isolated teeth. The taxonomic revision suggests that the delicate vertical ramus of the zygoma, the simplified p4 with an anterior flexid, and a variably developed metalophulid II are characteristic features. Ameghino (1891) erected the species *Acaremys karaikensis* on a very badly preserved skull of an adult specimen with simplified tooth morphology (MACN A 1885). The author considered that it was larger than *Acaremys murinus*, although having the tooth row of the same length. Nevertheless, specimens of intermediate size between *Acaremys murinus* and *Acaremys karaikensis* were posteriorly discovered (Scott 1905) and size differences are here dismissed as diagnostic since they represent intraspecific variability. Therefore, owing to the absence of other diagnostic tooth or skull characters, *Acaremys karaikensis* is considered here a junior synonym of *Acaremys murinus*. Finally, Ameghino (1891) stated that the mandible height in *Acaremys karaikensis* was 8.5 mm below the p4, but no mandible referable to this species was found at the MLP or MACN collections.

Acaremys messor and *Acaremys major* are poorly known because they are based on fragmentary remains. The cladistic analysis not corroborates or rejects their relationships with *Acaremys murinus*. We cannot certainly accept relationships involving zero-length branches, since all clades should be supported by characters (Coddington and Scharff 1994). Therefore, the original taxonomic assignment of *Acaremys major* and *Acaremys messor* is maintained here. Only more complete specimens will provide the information for solving their actual status. Besides the cranial and dental characters listed above, the identification of *Acaremys major* is evidenced by its size, being one of the largest fossil octodontoids so far known. *Acaremys messor* is characterised by having the cheek teeth longer than wide and a mandible with three mental foramina. Scott (1905) synonymised *Acaremys murinus* with *Acaremys messor* stating that the specimens referred to *Acaremys messor* were in fact larger specimens of *Acaremys murinus*. Here, we reject this hypothesis since

its diagnostic characters listed above are not present in other species.

Bordas (1939) erected the species *'Acaremys' preminutus*, which represented the oldest record of the genus so far (Colhuehuapian age). In an unpublished manuscript, Patterson (1952) synonymised *'Acaremys' preminutus* with the Patagonian octodontoid *Protacaremys prior* (Colhuehuapian age). Posteriorly, Wood and Patterson (1959) stated that *'Acaremys' preminutus* was an echimyid rejecting its relationships with *Acaremys*, although they did not refer it to any genus. The taxonomic revision and the cladistic analysis performed here corroborate that *'Acaremys' preminutus* is not an acaremyid, but it is closely related to *Protacaremys prior* (by having oblique crest and right anterolingual angle of the tooth on upper molars) or to the living octodontoids (by having longer than wide M2). A revision of the genus *Protacaremys* (being undertaken by one of the authors) is needed to formally justify the synonymy of *'Acaremys' preminutus* and *Protacaremys prior*, or its assignment as a new taxon.

'Acaremys' tricarinatus is represented by three mandibular remains and is characterised by having higher cheek teeth than the species of *Acaremys*, and a particular molar and mandibular morphology. Scott (1905) questioned the validity of this species and proposed that it could represent juvenile specimens of *Acaremys murinus*. Nevertheless, we have corroborated that the p4 morphology of *'Acaremys' tricarinatus* is not present in juvenile specimens of *Acaremys murinus* (flexid between metalophulid I and protoconid, metaconid anteriorly placed than protoconid and conspicuous hypolophid). Patterson (1952) in an unpublished manuscript synonymised *'Acaremys' tricarinatus* with *Sciamys principalis*. This last assumption should be tested in a revision of the genus *Sciamys*. Hitherto, we maintain the original systematic status of the species with quotations, indicating that it is not closely related to *Acaremys murinus*.

The new species, *Pseudoacaremys kramarzi*, is represented by an almost complete skull with dentition and two maxillary fragments with teeth. It has some unique cranial and dental features not shared with the remaining acaremyids (listed above). The specimens of this species were originally referred to *Acaremys murinus* by Ameghino (in Schedule) and Scott (1905). *Pseudoacaremys kramarzi* shares with *Acaremys* the presence of a sagittal crest and trilophodont upper premolar with a poorly developed hypoflexus. Nevertheless, it differs from *Acaremys* in the morphology of the ventral zygomatic root, the absence of furrow for the passage of the infraorbitalis nerve, the presence of a cusp embedded into the protoloph, the protoloph morphology on P4 and M3 and the still less development of the hypoflexus on P4. In addition, it differs from *Galileomys* in the crown height. The cladistic analysis demonstrated that this new species is not closely

related to *Acaremys murinus* but more closely related to *Sciamys*.

5.2 *Acaremyidae* and character evolution

The results of the phylogenetic analysis demonstrate that *Acaremyidae* is a monophyletic and an independent octodontoid lineage including *Platypittamys*, *Galileomys*, *Acaremys*, *Pseudoacaremys* and *Sciamys*. Concerning *Platypittamys*, besides its undoubtedly *acaremyid* dental morphology, its inclusion in the family should be studied in a broader taxonomic context because most analyses excluded it from this clade (Vucetich and Kramarz 2003; Arnal and Pérez 2013; Vucetich et al., *in press*). The description of a new *acaremyid* genus not only increases the systematic diversity of extinct octodontoids, but also added a new evolutionary lineage within the only extinct family described for Octodontoidea. As mentioned above, the monophyly of the family is supported by two synapomorphies, one has an unambiguous distribution (normal replacement of the deciduous premolar) and the other seems to have poorly evolutionary significance (position of hypocone on M3) since it evolved convergently with three other octodontoid lineages.

The octodontiform occlusal pattern was traditionally used to justify the close relationships of *acaremyids* as ancestors of modern octodontids (Wood and Patterson 1959; Pascual 1967). Nevertheless, this design is a frequent simplified morphology in proto to euhypsodont taxa and has been recorded in other rodents (Sénégal 2004; López-Antoñanzas and Knoll 2011). The evolutionary history of the superfamily recovered here explains that the eight-shaped occlusal pattern related to the increasing hypsodonty evolved at least twice within Octodontoidea: in the *Acaremyidae* and in modern Octodontidae [although not included in this analysis, eight-shaped occlusal pattern has also been convergently acquired in the Echimyidae lineage (Verzi et al. 1994)]. A difference between both families is that Octodontidae attained this pattern some time during Pliocene–Pleistocene interval and involves the reduction of the metalophulid II on lower molars, whereas among *acaremyids* the metalophulid II is complete and merges with the metalophulid I acquiring its occlusal pattern at least in the early Miocene.

It is noteworthy that according to this analysis most character ambiguities are due to missing data, not to a conflict between the characters. So, this highlights the need to find better remains to elucidate the relationships among *acaremyids*.

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