Article

A new acaremyid rodent (Hystricognathi: Octodontoidea) from the middle Miocene of Patagonia (South America) and considerations on the early evolution of Octodontoidea

MICHELLE ARNAL[1,2] & MARÍA E. PÉREZ[2,3]

[1]*Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, División Paleontología Vertebrados, Paseo del Bosque s/n, La Plata B1900FWA, Buenos Aires, Argentina. E-mail: michoarnal@fcnym.unlp.edu.ar.*
[2]*CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas)*
[3]*Museo Paleontológico Egidio Feruglio (MEF), Av. Fontana 140, Trelew U9100GYO, Chubut, Argentina. E-mail: mperez@mef.org.ar*

Abstract

Octodontoidea is the most speciose and ecologically diverse superfamily of caviomorph rodents. The systematic relationships of modern octodontoids is moderately accepted, however, the relationships of fossils (from the Eocene?–middle Miocene) are not clear. In recent years the hypothesis of a complex early evolution of the superfamily has emerged, with "basal octodontoids" representing different evolutionary lineages. The extinct family Acaremyidae may represent one such lineage, consisting of the genera *Acaremys*, *Sciamys*, *Galileomys*, and variably *Platypittamys*. In this work we describe a new octodontoid rodent recorded in post-Colloncuran? levels exposed at the locality of El Petiso, Northwest of Chubut Province, Argentina. Based on a systematic analysis of dental characters, we conclude that the new specimens correspond to a new species of *Sciamys*. Additionally, if the post-Colloncuran age for El Petiso is verified, the new species will extend the temporal range of the family Acaremyidae until, at least, the late middle Miocene, as well as the temporal range for the genus *Sciamys* from the Santacrucian SALMA. Our phylogenetic analyses corroborate the position of the new species as a member of *Sciamys*, and confirm that Acaremyidae represents an extinct family from Patagonian South America that lived until the middle Miocene. *Massoiamys obliquus* qualifies as morphological ancestor that pre-announces the octodontiform tooth pattern of octodontids. Thus, the octodontiform tooth pattern appears at least twice within the superfamily Octodontoidea.

Key words: Octodontoidea, Acaremyidae, phylogeny, Patagonia, middle Miocene

Introduction

The rodent clade Caviomorpha includes all hystricognath rodents that are endemic to the Neotropics, of which Octodontoidea is the most diverse superfamily (Reig 1989; Huchon & Douzery 2001). Extant octodontoids are traditionally grouped into Octodontidae, (including Ctenomyinae), Echimyidae, Myocastoridae, Abrocomidae, and Capromyidae (Simpson 1945; Huchon & Douzery 2001). Octodontids and echimyids are the most diverse and widespread octodontoids, occupying and exploiting most habitats in South America. Octodontidae is composed of octodontines (degus, rock rats, etc.) that inhabit arid and open regions from Peru to southern Patagonia, and ctenomyines (tuco-tucos) that inhabit a wider distribution but are primarily fossorial. Echimyidae (spiny rats, bamboo rats, etc.) inhabits tropical rainforest, savannas, thorn scrub, montane rainforest, and woodlands from Nicaragua to Northern Argentina and includes scansorial, arboreal, semifossorial and semiaquatic taxa (Ellerman 1940).

Although the systematic relationships of modern octodontoids are moderately accepted (Woods 1984; Huchon & Douzery 2001; Rowe *et al.* 2010), the relationships of "basal octodontoids" (i.e. those of Eocene?–middle Miocene faunas) are not clear, even though they have been widely studied (Ameghino 1887, 1889, 1902; Scott 1905; Wood 1949; Wood & Patterson 1959; Patterson & Pascual 1968; Patterson & Wood 1982; Vucetich & Kramarz 2003; Frailey & Campbell 2004; Vucetich *et al.* 2010a, b). Traditionally, the history of this superfamily

was suggested as characterized by an early dichotomy that gave rise to the Echimyidae and Octodontidae lineages (Wood & Patterson 1959; Patterson & Pascual 1968; Patterson & Wood 1982; Vucetich & Verzi 1991). Nevertheless, in recent years an alternative hypothesis has proposed a complex early evolution of the superfamily with "basal octodontoids" representing different evolutionary lineages not represented in the modern faunas (Vucetich & Kramarz 2003; Vucetich & Ribeiro 2003; Carvalho & Salles 2004; Vucetich & Vieytes 2006; Arnal 2012).

Acaremyidae would represent one of those lineages and was established as a family by Wood (1949), who considered it as the ancestral stock of Cavioidea, Chinchilloidea and Octodontoidea. Nonetheless, the incisor enamel microstructure suggests that Acaremyidae belongs within Octodontoidea (Martin 1992). Numerous authors (Wood 1955; Wood & Patterson 1959; Pascual 1967; Woods 1984) referred the acaremyids to the Octodontidae because both groups share a figure-eight occlusal pattern. However, based on a cladistic analysis, Vucetich & Kramarz (2003) proposed that Acaremyidae represents an extinct early radiation of Octodontoidea including *Acaremys* Ameghino, 1887, *Sciamys* Ameghino, 1887 and *Galileomys* Vucetich & Kramarz, 2003, but excluding *Platypittamys* Wood, 1949. Thus, following those authors, acaremyids were recognized from the Colhuehuapian South American Land Mammal Age (SALMA) (early Miocene) until the Santacrucian SALMA (latest early Miocene). Among the acaremyids recognized from the Colhuehuapian are *Galileomys antelucanus* Vucetich & Kramarz, 2003 and *Acaremys* cf. *murinus* by Vucetich & Kramarz (2003). In the "Pinturan" Age *Galileomys eurygnathus* (Kramarz 2004) is recognized, and in the Santacrucian SALMA five nominal species of *Acaremys* (Ameghino 1887, 1889, 1891, 1894; Scott 1905) and five other *Sciamys* (Ameghino 1887, 1894; Scott 1905) are recognized. One species described as *Galileomys*? *colloncurensis* was recognized for the middle Miocene (Colloncuran Age) (Vucetich & Kramarz 2003). Nevertheless, this generic assignation is tentative owing to the incompleteness and poor preservation of the specimens.

In this contribution we described a new species of *Sciamys* represented by lower cheek teeth and mandibular remains. These specimens were recorded in post-Colloncuran? and pre-Chasicoan levels exposed at the locality of El Petiso, Northwest of Chubut Province, Argentina (Fig. 1; Villafañe *et al.* 2008). A cladistic analysis was performed in order to study the relationships of this new species within the Octodontoidea in a broad sense, and specifically within the Acaremyidae.

Material and methods

Tooth nomenclature follows Vucetich & Ribeiro (2003), Marivaux *et al.* (2004), and Candela & Rasia (2011). Mandibular nomenclature follows Wible *et al.* (2005). For the identification of some structures in the tooth pattern we follow the concepts of topology and connectivity (Rieppel 1994).

We examined specimens deposited in the following collections: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Ameghino, Buenos Aires, Argentina (MACN A); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Paleontología de Vertebrados, Buenos Aires, Argentina (MACN PV); Museo de La Plata, La Plata, Argentina (MLP); Museo Paleontológico Egidio Feruglio, Paleontología de Vertebrados, Trelew, Argentina (MPEF-PV); and Yale Peabody Museum, University of Princeton, New Haven, USA (YPM PU).

Phylogenetic analysis. The phylogenetic relationships of the new species were assessed using a modified version of the dataset of Vucetich & Kramarz (2003). This dataset (see Appendix 1) encompassed a total of 15 taxa (Table 2) scored for 20 morphological characters (see Appendix 2), six of which were modified from the original dataset and three of which are new characters added in this study (character 4, presence or absence of roots; character 8, metaloph on M1-M3; character 17, anteroposterior length of the anterior lobe on m1-m2 with respect to the anteroposterior length of posterior lobe). Two multistate characters (5 and 14) were considered as additive based on the increasing degrees of similarity between adjacent character states. Furthermore, one character (degree of hypsodonty [char.1]) was treated as continuous following the methodology proposed by Goloboff *et al.* (2006) (see Table 1). Characters have been scaled multiplying them by 2. The taxon sampling included the new species of *Sciamys*, three acaremyids, seven octodontoids *incertae sedis*, and three octodontids (*sensu* Vucetich & Kramarz 2003) (see Table 2). The phylogenetic trees were rooted with a "phiomorph" rodent, *Phiomys andrewsi*.

This dataset was analyzed using equally weighted parsimony in TNT 1.1 (Goloboff *et al.* 2008a, b), a method that minimizes the number of postulated evolutionary transformations. We performed a branch-and-bound search algorithm (implicit enumeration in TNT), which warrants finding all most parsimonious trees for a given dataset. Support values were calculated using Bremer and Jackknife indices (the latter is a resampling technique that is summarized using absolute frequencies and GC frequencies; see Goloboff *et al.* 2003). Bremer support was calculated using the script BREMER.RUN provided with TNT and resampling techniques were conducted performing 1000 pseudoreplicates.

TABLE 1. Dental measurements of *S. petisensis*, including the hypsodonty index (HI). Measurements are in milimeters and were taken in juvenile specimens. Abbreviations: A-P= antero-posterior length of the occlusal surface; AW= anterior transverse; CH= crown height; PW= posterior transverse. CH and PW were measured at the level of the protoconid.

SPECIES	SPECIMEN		CH	A-P	HI (CH/A-P)	AW	PW
Acaremys murinus	MACN A 266	m1	1.05	1.80	0.583		
		m2	1.15	1.90	0.605		
	MACN A 1879	m1	1.65	2.15	0.767		
		m2	1.40	2.20	0.636		
Chasichimys bonaerense	MLP 55-IV-28-99	m2	2.50	2.06	1.213		
Eumysops laeviplicatus	MACN A 7314	m2	4.00	3.72	1.075		
Galileomys antelucanus	MPEF-PV 5993	m1	1.60	1.70	0.941		
Migraveramus beatus	YPM PU 21948	m1	1.45	2.25	0.640		
Phiomys andrewsi	YPM PU 18071	m2	16.78	35.98	0.466		
Protacaremys prior	MACN A 52-112b	m1	1.06	1.80	0.588		
		m2	1.08	1.94	0.556		
Sciamys petisensis	MPEF-PV 3560	p4		2.1		1.6	2.1
		m1		2.4		2.1	2.1
		m2		2.3		1.9	2.0
		m3		2.2		1.7	1.5
		dp4		2.9		1.4	1.7
	MPEF-PV 3561	m1	3.20	2.10	1.523	1.5	1.3
	MPEF-PV 3562	p4		2.5		1.9	2.5
		m1		2.4		2.5	2.5
		m2		2.5		2.6	2.6
		m3		2.3		2.3	2.0
	MPEF-PV 3563	m1		2.1		2.2	2.2
		m2		2.2		2.4	2.3
		m3		2.1		2.0	1.6
	MPEF-PV 3564	m2		2.5		2.3	2.2
	MPEF-PV 3565	m1		2.4			
	MPEF-PV 3566	dp4					1.8
		m1		2.4		2.0	2.1
		m2		2.1		2.0	1.8
Sciamys principalis	MACN A 4107	m1	2.00	2.20	0.909		
	MACN PV SC2588	m1/m2	2.20	1.96	1.132		
	MACN PV SC2588	m1/m2	2.30	1.98	1.161		
Stichomys regularis	MACN A 4198	m1	2.22	3.26	0.681		

TABLE 2. Taxa used for the Phylogenetic Analysis († = extinct).

Family	Species
"Phiomorpha"	†*Phiomys andrewsi* Osborn 1908
Octodontoidea incertae sedis	†*Platypittamys brachyodon* Wood 1949
	†*Migraveramus beatus* Patterson & Wood 1982
	†*Protacaremys prior* Ameghino 1902
	†*Deseadomys arambourgi* Wood & Patterson 1959
	†*Eumysops laeviplicatus* Ameghino 1888
	†*Stichomys regularis* Ameghino 1887
	† *Massoiamys obliquus* Vucetich 1978
Acaremyidae	†*Galileomys antelucanus* Vucetich & Kramarz 2003
	† *Acaremys murinus* Ameghino 1887
	†*Sciamys principalis* Ameghino 1887
	†*Sciamys petisensis* **sp. nov.**
Octodontidae	†*Chasicomys octodontiforme* Pascual 1967
	†*Chasichimys bonaerense* Pascual 1967
	Octomys mimax Thomas 1920
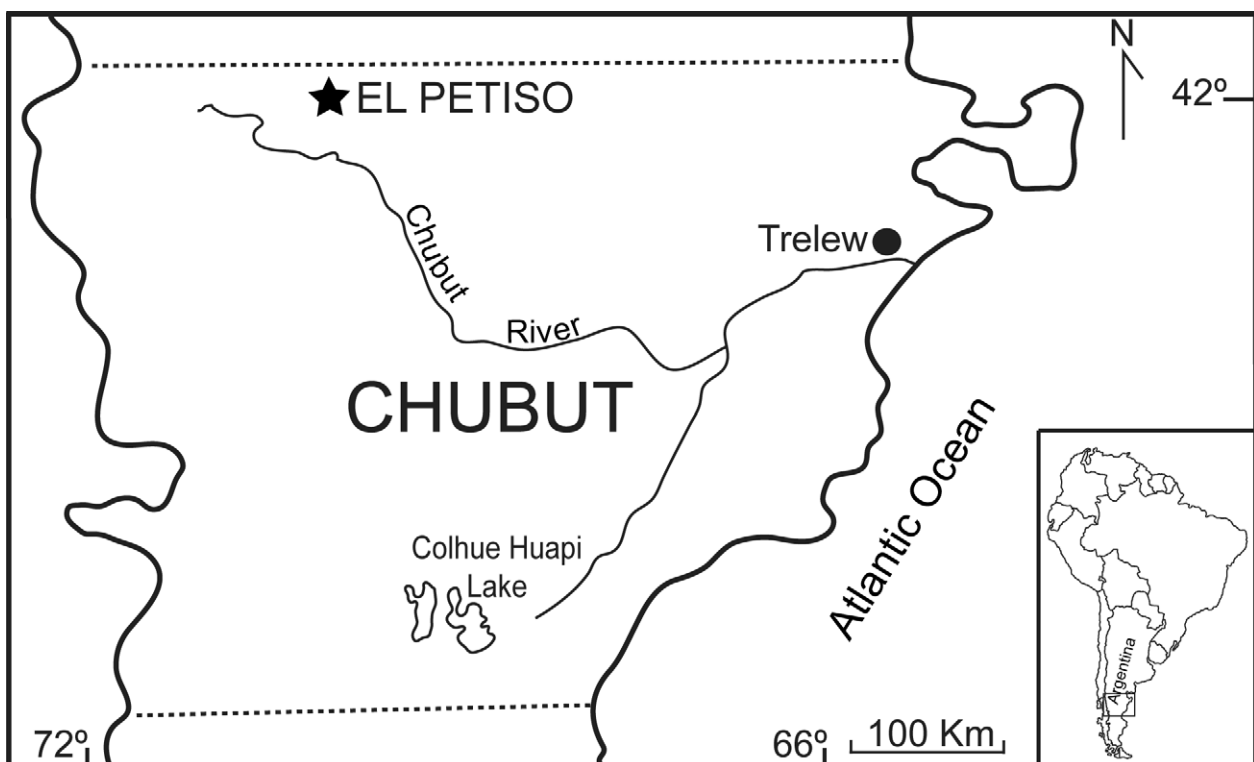
FIGURE 1. Location map of El Petiso Locality (Chubut Province), Argentina.

Results

Systematic paleontology

Rodentia Bowdich, 1821

Hystricognathi Tullberg, 1899

Octodontoidea Waterhouse, 1839

Sciamys Ameghino, 1887

Included species. *Sciamys principalis* Ameghino, 1887, Santacrucian; *Sciamys varians* Ameghino, 1887, Santacrucian; *Sciamys robustus* Ameghino, 1894, Santacrucian; *Sciamys rostratus* Scott, 1905, Santacrucian; *Sciamys latidens* Scott, 1905, Santacrucian.

Sciamys petisensis **sp. nov.**
(Figures 2A, 3A, 4)

Holotype. MPEF-PV 3560, right mandibular fragment with p4-m3.

Referred material. MPEF-PV 3561, right mandibular fragment with dp4-m1; MPEF-PV 3562, left mandibular fragment with p4-m3; MPEF-PV 3563, left mandibular fragment with m1-m3; MPEF-PV 3564, right mandibular fragment with i, posterior lobe of m1, and m2; MPEF-PV 3565, right mandibular fragment with i, posterior lobe of m1, and m2; MPEF-PV 3566, left mandibular fragment with i, dp4-m2.

Diagnosis. Medium size octodontoid, somewhat larger and higher crowned than *Sciamys principalis, Galileomys antelucanus,* and *Acaremys murinus*; dp4 with the posterolabial corner of the protoconid forming a right angle; p4 with an ephemeral or without a flexid on the anterior face of the tooth separating protoconid from metaconid unlike other acaremyids, mesolophid? more developed than in *S. principalis*, and rudimentary hypolophid. Molars with metalophulid II longer and extending from the ectolophid in a more posterior position, near the hypolophid, delimiting a broader anterofossettid than in others acaremyids. Mandible with the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle oblique anterodorsal–posteroventrally and aligned with the masseteric crest, unlike *S. principalis*. Anterior portion of the masseteric fossa shallower than in *A. murinus*.

Locality and horizon. Materials were found in the locality El Petiso, Northwestern of Chubut Province, central Patagonia, Argentina (Fig. 1; Villafañe *et al.* 2008; Pérez 2010). The faunal assemblage found at this locality indicates a middle Miocene age, probably post-Colloncuran (early–middle Miocene; Villafañe *et al.* 2008). Precise coordinates of the fossiliferous locality of the type material are housed at the MPEF-PV collections and can be obtained from one of the author (MEP) upon request.

Etymology. The specific epithet refers to the locality name "El Petiso" (Chubut Province, Argentina).

Description and comparison. The cheek teeth of *Sciamys petisensis* are higher crowned than in other acaremyids (Table 1). Cusps are strongly embedded within crests, unlike the species of *Galileomys*, *Acaremys*, and *S. latidens*.

Lower deciduous premolar. The dp4 morphology is in general terms as in *S. principalis* and *A. murinus*, and unlike *G. eurygnathus* (dp4 of the type species of *Galileomys*, *G. antelucanus*, are unknown), since it has a well developed metalophulid II, and a reduced mesolophid.

The dp4 present a metalophulid I and a mesolophid delimiting an anterior lobe, as in other acaremyids. The ectolophid is very oblique and extends from the protoconid to the anterior arm of the hypoconid (Fig. 2A). The mesolophid is long, unlike *G. eurygnathus*, and extends from the ectolophid near the hypolophid in a more posterior position than in *S. principalis* and *A. murinus* (Fig. 2A–B). In juvenile specimens the anterofossettid is divided by an anterior-posterior oriented crest of uncertain homologies (neolophid?, Candela 2002; metalophulid II?, Arnal 2012), because it is not possible to distinguish if this crest is an anterior extension of the mesolophid as in *S. principalis* (Fig. 2B) and *A. murinus*, or a posterior extension of the metalophulid I. The lingual fossettid is shallower than the labial one, and disappears with little wear (in Fig. 2A this fossetid is nearly unnoticeable), while in *S. principalis* it is evident in the same stage of wear. Unlike other acaremyids, the posterolabial corner of the protocone forms a right angle (Fig. 2A). The hypolophid extends lingually from the point where the ectolophid contacts the anterior arm of the hypocone, and reaches the lingual margin of the tooth. The posterolophid is anteriorly concave and is as long (transversally) as the hypolophid. The mesoflexid penetrates half of the crown, and is more posteriorly oriented and narrower than *S. principalis* (Fig. 2A–B). The posteroflexid is transverse, and is as deep and penetrating as the mesoflexid, like *G. eurygnathus* and unlike *S. principalis* and *A. murinus*. The hypoflexid is the deepest and broadest of all flexids.
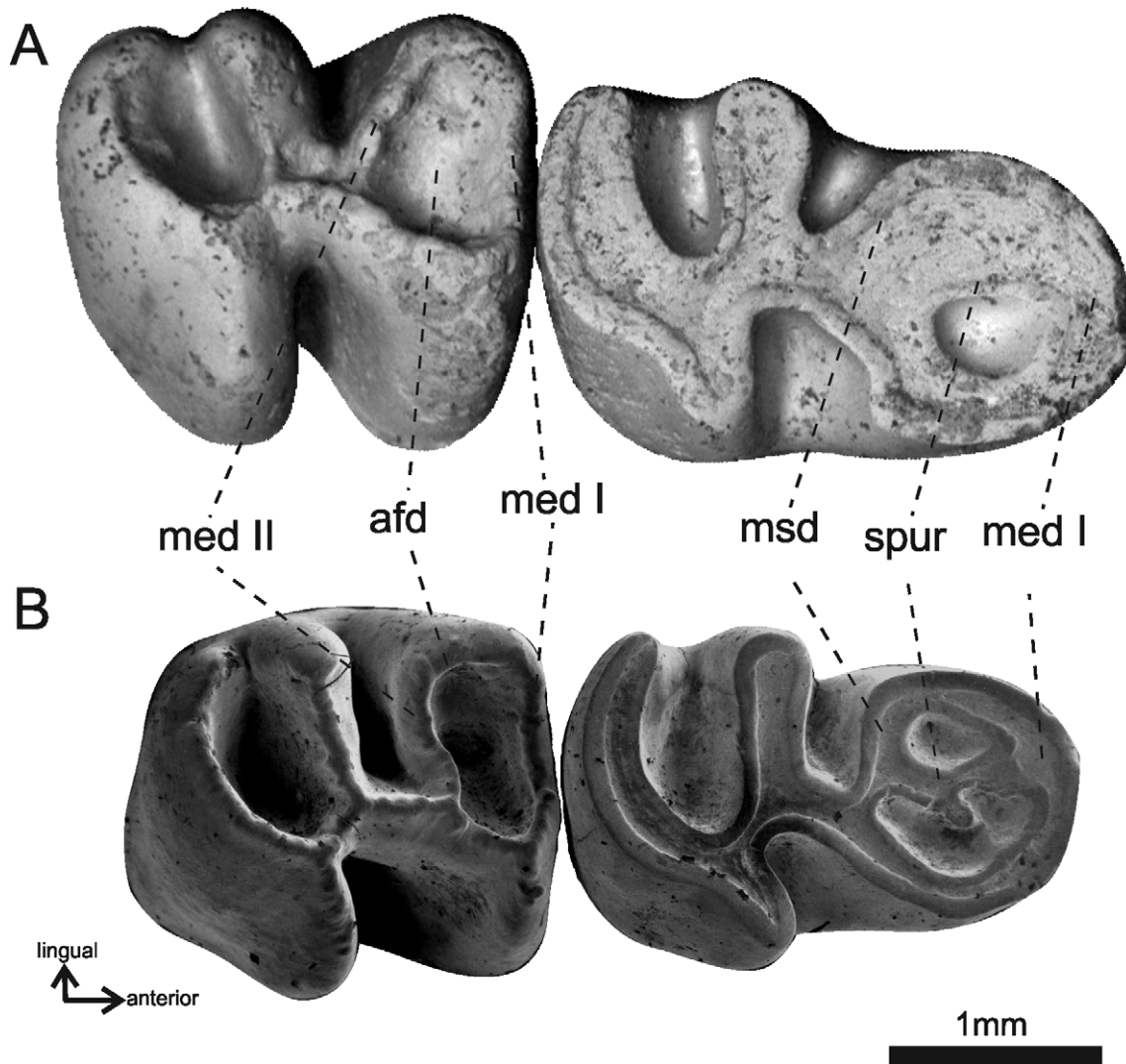
FIGURE 2. Comparison between *Sciamys petisensis* and *Sciamys principalis*. *S. petisensis*, MPEF-PV 3561, right dp4-m1 (A), and *S. principalis*, MACN PV SC 2394, right dp4-m1 (B). Abbreviations: **afd**, anterofossettid; **med I**, metalophulid I; **med II**, metalophulid II. Scale bars equal 1mm.

Lower permanent premolar. The p4 is more complex than in most acaremyids, except for some specimens of *S. principalis*, and has the typical acaremyid morphology (Vucetich & Ribeiro 2003). In the holotype of *S. petisensis* (MPEF-PV 3560) the metalophulid I is complete and there is no a flexid separating protoconid and metaconid (Fig. 3A). Nevertheless, this could be by the presence of a minute flexid that disappears rapidly with wear, or by the absence of such a flexid. Regardless the case, it differs from the species of *Galileomys*, *Acaremys* and most specimens of *Sciamys*, where this flexid is conspicuous. From the posterior border of the protoconid extends the ectolophid that is oblique and reaches the posterolophid. A second crest in position, anterolingually oriented, extends from the ectolophid to the metaconid, delimiting a subcircular anterofossettid (Fig. 3A). This crest seems to correspond to the mesolophid of some specimens assigned to *S. principalis* (Fig. 3B) and *S. varians*, and its identification is based on its more posterior origin in the ectolophid (the metalophulid II, or the posterior arm of the protoconid, would has an anterior origin). An anteriorly concave posterolophid delimits the posterior rim of the tooth, as in other acaremyids. *S. petisensis* has a small hypolophid (Fig. 3A) as in *S. principalis* and *S. varians*, and unlike *S. latidens,* that is separated from the posterolophid by a minute flexid.

Lower molars. Molar morphology of *S. petisensis* is similar to other acaremyids, with a few differences (Fig. 2 and 3). Metalophulid I unites protoconid and metaconid and is straight, unlike *S. latidens* where this crest is oblique. Metalophulid II is long; unlike other acaremyids, it contacts the ectolophid in a posterior position, near the hypolophid, and extends to the metaconid delimiting a broader anterofossettid than in the species of *Sciamys* (Fig.

ARNAL & PÉREZ

2A–B). This anterofossettid disappears with little wear (Fig. 3A). This is the most important character that differentiate the molars of this new species from others acaremyids; nevertheless, it is only evident in teeth without or with little wear. The posterolophid is long, reaching the lingual margin of the tooth, as in the species of *Sciamys* and *Acaremys*, and unlike species of *Galileomys* and *Platypittamys brachyodon*. As in the dp4, the mesoflexid is little more penetrating and deeper than the posteroflexid. Hypoflexid is little posteriorly oblique and is the broadest and deepest of all flexids. As is usual in octodontoids, m3 is labio-lingually shorter in its posterior half. This is due to a shorter posterolophid and the lingual position of the hypocone respect the protocone (Fig. 3A).
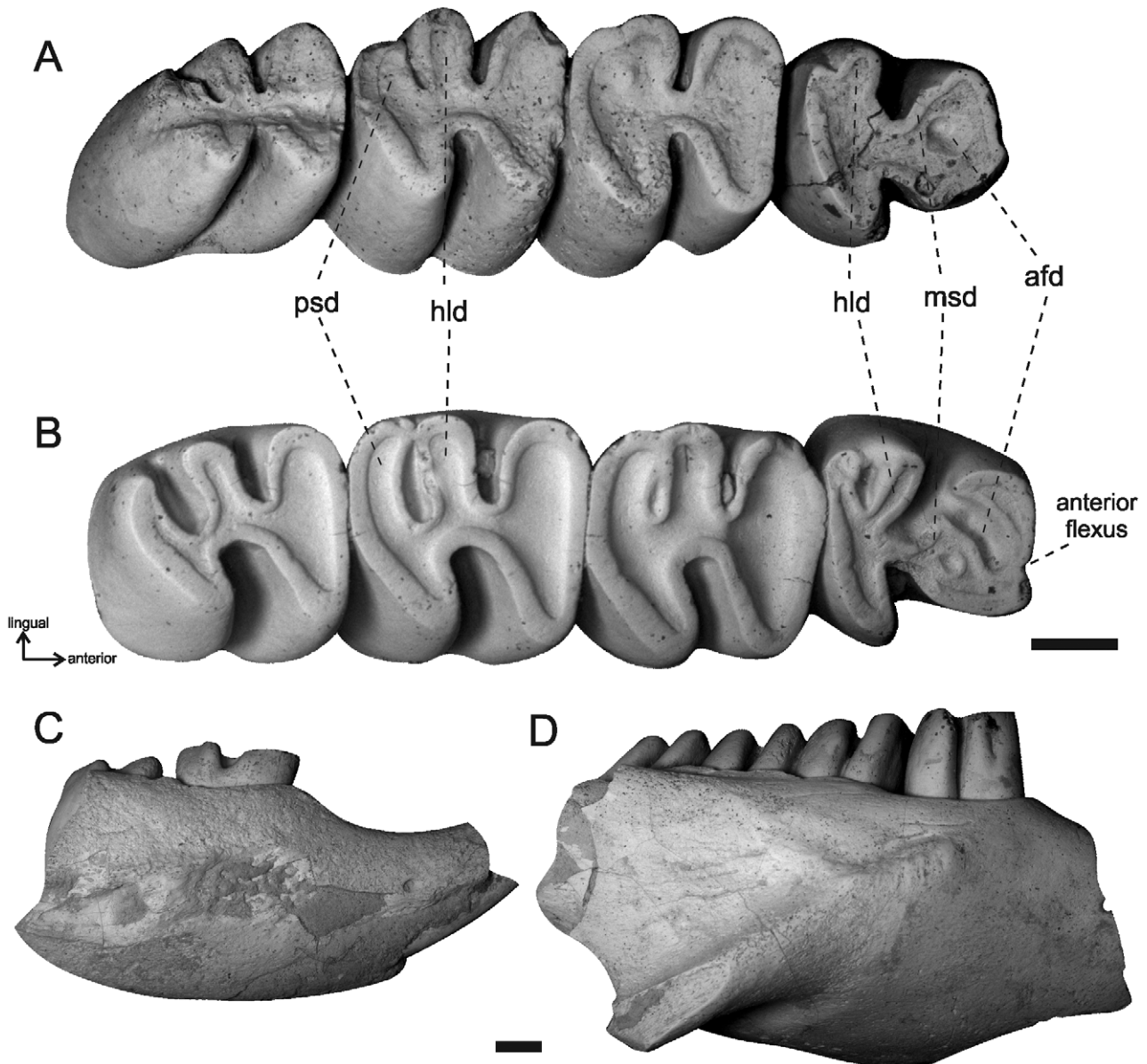

FIGURE 3. *Sciamys petisensis*, MPEF-PV 3560 (Holotype), right p4-m3 (A); *Sciamys principalis*, MACN PV FSC2314, right p4-m3 (B); *S. petisensis*, MPEF-PV 3561, right mandible with dp4-m1 (C); *S. petisensis*, MPEF-PV 3560, right mandible with p4-m3 (D). Abbreviations: **afd**, anterofossettid; **hld**, hypolophid; **maf**, masseteric fossa; **mf**, metal foramen; **mmpim**, insertion for the tendon of the masseter medialis pars infraorbitalis muscle; **msd**, mesolophid; **psd**, posterolophid. Scale bars equal 1mm.

Incisors. In most specimens of *S. petisensis*, incisors are broken near the outer border of their alveolus. In the specimen MPEF-PV 3566 the incisor is oval in section (the tooth is broken off above m1 alveolus). The anterior face of the tooth forms a straight medial angle, being the lateral one curved. The incisors are long and extend below the tooth row as far as m3, where they rise up to the coronoid process, as is usual in acaremyids.

Mandible. Available dentaries have some damage, and the posterior part is not preserved in any specimen. The

body of the mandible, the tooth bearing horizontal part, is high and broad. Anterior to the tooth row the diastema is concave and not very deep (Fig. 3C). The mental foramen is well developed and is located slightly in front of the deepest point of the diastema, far from the p4 (Fig. 3C). The notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (*sensu* Woods & Howland 1979) is long anteroposteriorly, and lies beneath p4-m1 (Fig. 3D); it is oblique unlike in species of *Sciamys*, and is continuously aligned with the masseteric crest (Fig. 3D). The masseteric fossa extends forward beneath the anterior lobe of the m1 and its anterior portion is shallower than in *A. murinus*, *G. antelucanus*, and *G. eurygnathus*. In the posterodorsal portion of the fossa is a rounded prominence that corresponds to the base of the incisor. The coronoid process rises at the m3 level, and the retromolar fossa (*sensu* Woods & Howland 1979) is mostly posterior to the tooth row.

Dental Ontogeny. The availability of specimens with different stages of wear enables us to study the ontogenetic sequences of flexid closure, as well the formation and disappearance of fossettids (Fig. 4).
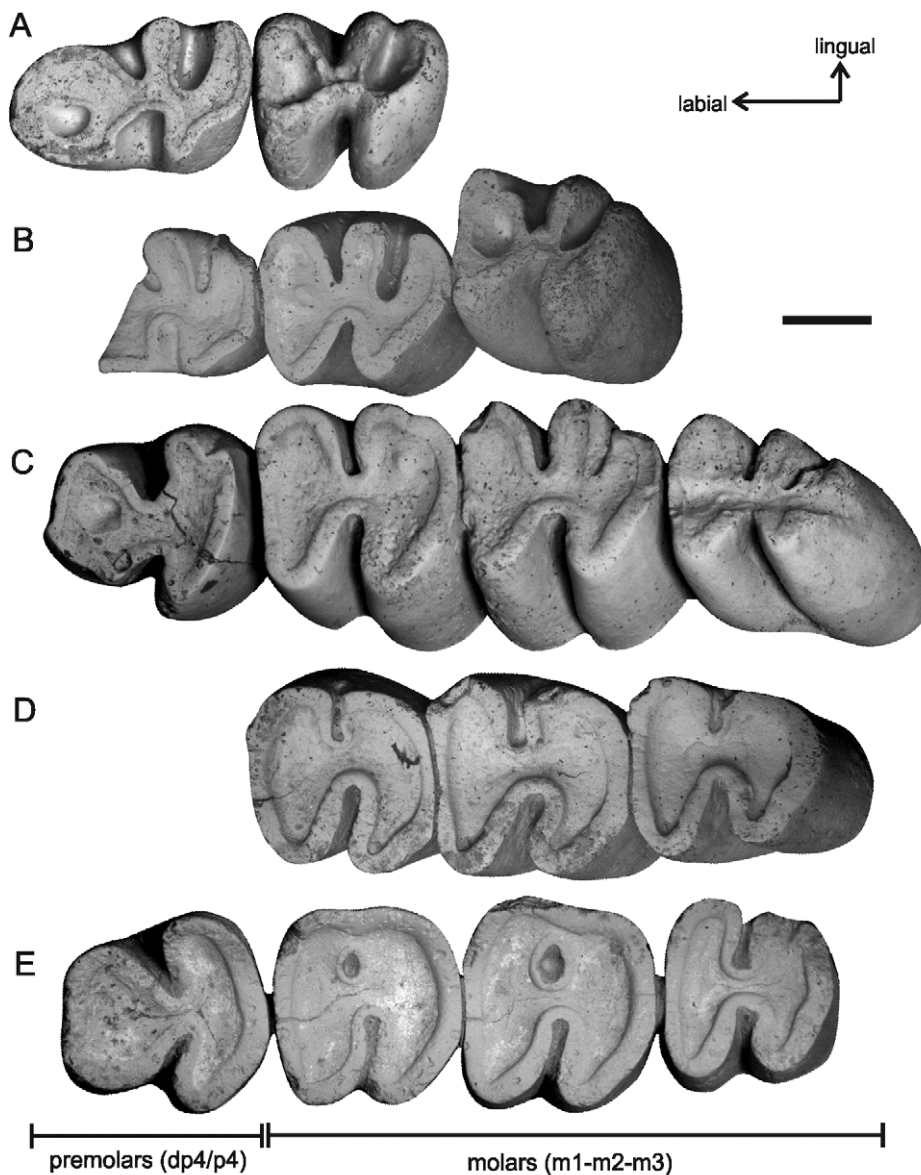
FIGURE 4. Ontogenetic series showing the transitional octodontiform molar pattern in *S. petisensis* sp. nov. MPEF-PV 3561, right dp4-m1 (shown as left) (A); MPEF-PV 3563, left dp4 (partially preserved)-m2 (B); MPEF-PV 3560, right p4-m3 (shown as left) (C); MPEF-PV 3566, left m1-m3 (D); MPEF-PV 3562, left p4-m3 (E). Scale bars equal 1mm.

The MPEF-PV 3561 and MPEF-PV 3563 (Fig. 4A–B) represent the most juvenile available specimens, since both retain the dp4. Of the two fossettids present in the anterofossettid of the dp4, the lingual one is shallower and disappears with little wear (Fig. 4A). With a little more wear the labial fossetid disappears (Fig. 4B). In MPEF-PV

3561 (an almost unworn specimen) the posteroflexid is broad and more penetrating than the mesoflexid, while in MPEF-PV 3563, which is little more-worn, the posteroflexid is narrower and less penetrating than the mesoflexid. In MPEF-PV 3561 the hypoflexid is wide, with its anterior border nearly C shaped (Fig. 4A), while in MPEF-PV 3563 it is much narrower and U shape (Fig. 4B).

The holotype (MPEF-PV 3560) and the specimen MPEF-PV 3562 had replaced the deciduous premolars by permanent ones. Little-worn p4s have conspicuous anterofossettid and a distinct hypolophid (Fig. 4C), while in more-worn premolars the anterofossettid is entirely worn away and the hypolophid is fused with the posterolophid, resulting in a simplified occlusal surface (Fig. 4E).

Unworn molars have a broad and shallow anterofossettid (Fig. 4A) that disappears with little wear (Fig. 4B-C). The posterolophid is long and seems to reach the lingual border of the tooth. The posteroflexid is broad and deep in unworn specimens, but with little wear it becomes narrower and less penetrating in the occlusal surface (Fig. 4B), and in adult specimens it is transformed into an ephemeral posterofossettid (Fig. 4C) that rapidly disappears (Fig. 4D-E). In worn molars (Fig. 4D) a temporary octodontiform occlusal pattern is observable, as in other acaremyids, which has led many authors to propose the acaremyids as being octodontids, or the ancestors of modern octodontids (Wood & Patterson 1959; Pascual 1967; Patterson & Wood 1982). Nevertheless, the octodontiform pattern present in acaremyids and octodontids is not homologous; in acaremyids the lingual flexid corresponds to the mesoflexid while in octodontids it is the mesoflexid+anteroflexid (the metalophulid II is reduced or absent in the latter). In most-worn specimens (Fig. 4E) the mesoflexid is transformed into mesofossettid, except in m3, where an octodontiform molar pattern is still present (Fig. 4E). The hypoflexid is the deepest flexid; in most-worn specimens it remains open, and becomes more straight and transverse (Fig. 4E).

Phylogenetic analysis. The parsimony analysis resulted in one most parsimonious tree (MPT) of 40.178 steps (CI=0.600 RI=0.727). The decimal values in the Tree lengths correspond to the use of a continuous character for the character on the degree of hypdodonty (see above). The MPT is shown in Figure 5. The only most parsimonious hypothesis of this analysis found Acaremyidae to be a monophyletic group (Fig. 5), and placed *Sciamys petisensis* in a sister relationship with *S. principalis* (Fig. 5, node 7), thereby justifying the generic assignment of the new taxon. One unambiguous synapomorphy supports this clade in the MPT: cusps not distinguishable from their respective crests (character 2[1]). *Galileomys antelucanus* is the sister group of *Sciamys* (Fig. 5, node 6), and one unambiguous synapomorphy supports its position: degree of hypsodonty larger than 0.9 (character 1[0.941]).

Acaremys murinus is the basalmost species of Acaremyidae, and four unambiguous synapomorphies support this clade in the MPT: 1) hypoflexus in the upper premolar poorly developed (character 5[1]); 2) presence of the figure-eight-shaped in the upper cheek teeth (character 7[1]); 3) presence of the figure-eight-shaped in the lower cheek teeth (character 13[1]); and, 4) presence of a conspicuous anterodorsal limit of the mandibular masseteric fossa (character 19[1]).

The topology obtained in this analysis coincides with the results of Vucetich & Kramarz (2003), in retrieving a monophyletic Acaremyidae, which is supported by the same unambiguous synapomorphies (see Appendix 3). Here, we decided to consider the figure-eight-shaped occlusal surface of the lower and upper cheek teeth as two separated characters (character 7, and 13), given that *Massoiamys obliquus* presents a different condition in the upper and lower toothrow [lower tooth presents an octodontiform molar pattern (MLP 76-VIII-30-2), but the upper tooth does not (MPL 91-V-1-36)], demonstrating that these two characters varied independently in the evolutionary history of the group. On the other hand, unlike the results of Vucetich & Kramarz (2003), *Sciamys* is depicted in our analysis as more closely related to *Galileomys*, whereas *Acaremys* is the basalmost taxa of this clade. The grouping of *G. antelucanus* and *Sciamys* is supported by their more developed degree of hypsodonty (c.1), as reflected by the hypsodonty index that here we treated as a continuous character.

The support values in the strict consensus are low, but Acaremyidae is the node with the highest support values (Bremer = 1.602; jackknife absolute frequency = 69; jackknife GC frequency = 66; see fig. 5, node 5). The relationships within Acaremyidae are not strongly supported within the context of this dataset, and the treatment of the hypsodonty index as a continuous character provides information to resolve their relationships in absence of other phylogenetically informative discrete characters. It has been noted that the use of continuous characters avoids making arbitrary character state delimitations (Goloboff *et al.* 2006) but also their use allows using subtle morphological variations at low taxonomic levels (Escapa & Pol 2011). This is reflected in the support values of the groups within Acaremyidae. For instance the clade of *Galileomys*+*Sciamys* has lower support values (Bremer =

0.348; jackknife absolute frequency < 20; jackknife GC frequency = 19; see fig. 5, node 6) because the close affinity of these taxa is mostly the result of being the acaremyids with the highest degree of hypsodonty. Discrete morphological characters provide the basis for their inclusion in this family (see synapomorphic features of Acaremyidae above), whereas the continuous character is critical for resolving the internal relationships within this clade. This also happens in the *Sciamys* clade (i.e., *S. petisensis* + *S. principalis*) where nodal support is low (Bremer = 0.348; jackknife absolute frequency < 20; jackknife GC frequency = 21; see fig. 5, node 7), but the affinity of these two species results from both having a high hypsodonty index (see Table 1).
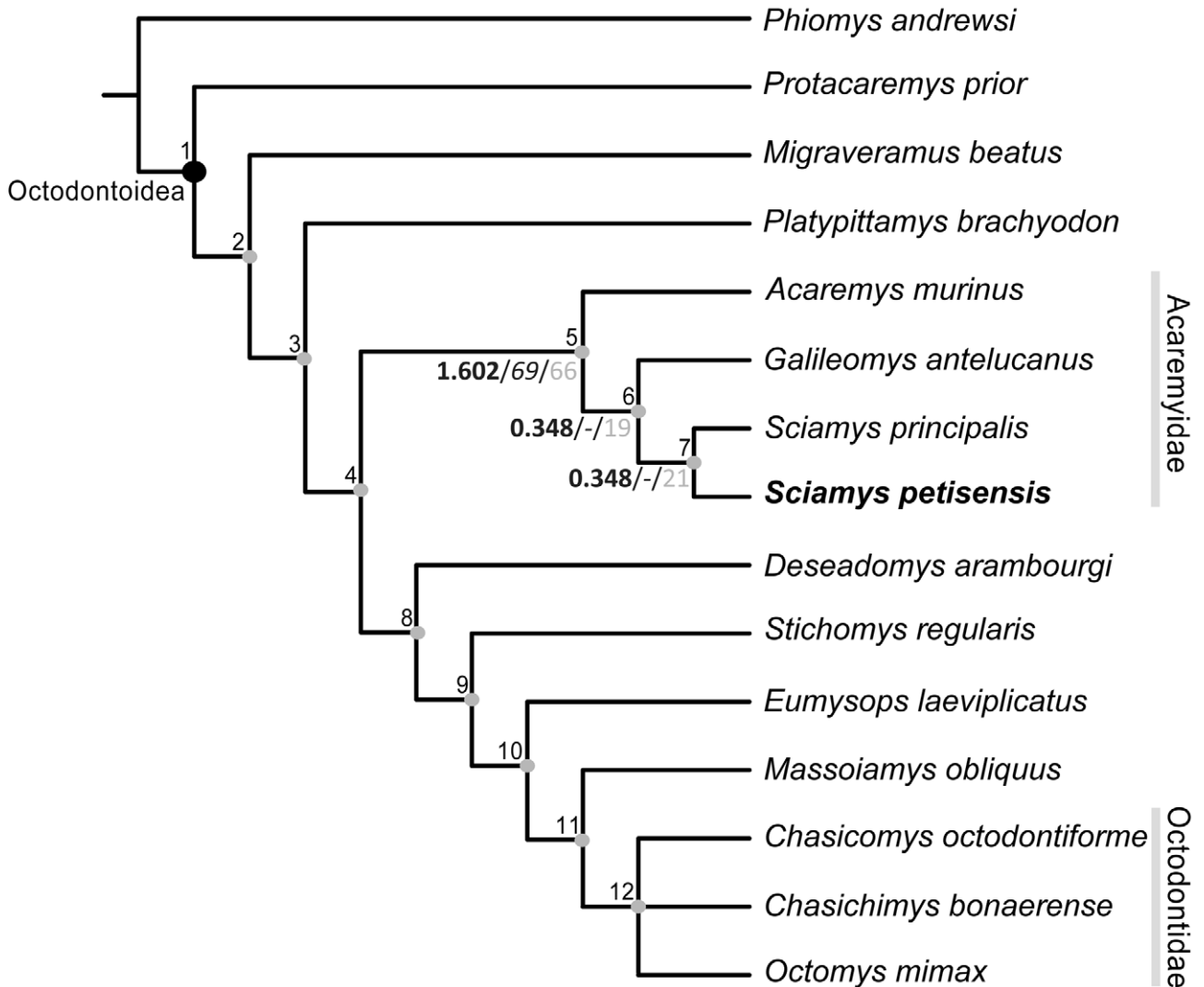
FIGURE 5. Strict consensus of the most parsimonious tree (Length=40.178; CI=0.600, RI=0.727) resulting from cladistic analysis of a modified matrix of Vucetich & Kramarz (2003). The numbers in bold indicate Bremer indices, numbers in italics represent absolute Jackknife values, and numbers in gray represent GC Jackknife values.

These cases exemplify the potential use of continuous characters for resolving phylogenetic problems in the absence of large morphological variation, or when examining partially preserved remains in fossil taxa. Continuous characters can be especially useful at low taxonomic scales (Escapa & Pol 2011). In such cases, phylogenetic hypotheses are bound to have low support values, but are nonetheless the most parsimonious interpretation of the available data. For instance, if *S. petisensis* were located elsewhere within the clade Acaremyidae, it would imply that the high hypsodonty of this taxon was acquired independently from that of *S. principalis* (or that this character had a reversal in other members of the family). Previous cladistic analyses (Vucetich & Kramarz 2003; Pérez 2010; Pérez & Pol 2012) treated the degree of hypsodonty as a discrete character, building arbitrary characters states (generally poorly defined). Nevertheless, the results obtained by Vucetich & Kramarz (2003) showed the internal relationships of Acaremyidae totally resolved using the hypsodont index as a discrete character. Our use of a

continuous character to describe degree of hypsodonty is a first in studies of fossil rodents. While all measurements should ideally be taken in specimens without wear, we have taken the measurements in juvenile specimens with the least possible wear.

Discussion

Taxonomic and phylogenetic analyses found that the new octodontoid specimens of El Petiso represent a new species of *Sciamys*. *Sciamys petisensis* shares with the species of *Sciamys* some derived features for octodontoids, as the higher degree of hypsodonty, cusps not individualized (this feature is absent in *S. latidens*), complex p4, and the masseteric fossa shallower than in the species of *Acaremys* and *Galileomys*. However, along with these similarities, it differs from the remaining species of *Sciamys* by the higher degree of hypsodonty, the absence or the presence of an ephemeral flexid separating protoconid and metaconid in p4, the position of metalophulid II in lower molars, and the position of the notch for the tendon of the masseter medialis pars infraorbitalis muscle in the mandible.

The phylogenetic analysis confirms that Acaremyidae is monophyletic and an independent lineage within Octodontoidea. This result reinforces the idea of a complex early evolutionary history of the superfamily (Vucetich & Kramarz 2003; Vucetich & Ribeiro 2003; Vucetich & Vieytes 2006; Vucetich *et al.* 2010a; Arnal 2012), and replaces the traditional view of a deep basal dichotomy into Echimyidae and Octodontidae (Wood & Patterson 1959; Patterson & Wood 1982; Vucetich & Verzi 1991; Vucetich *et al.* 2011). The broader phylogenetic position of Acaremyidae relative to other fossil and living taxa in Octodontoidea remains controversial and is beyond the scope of this work.

The Colloncuran (early middle Miocene) *Galileomys*? *colloncurensis* was thus far the most recent record of an acaremyid (Vucetich & Kramarz 2003). The mammal assemblage found in El Petiso suggests a post-Colloncuran Age (Villafañe *et al.* 2008; Pérez 2010). If this age is verified, *S. petisensis* will extend the temporal range of the family Acaremyidae until, at least, the middle middle Miocene [c.a. 13.8 Ma based on Colloncuran (Vucetich *et al.* 1993) and Laventan ages (Madden *et al.* 1997)]. Further, the new species extends the temporal range for the genus *Sciamys* beyond the Santacrucian SALMA.

By the middle Miocene octodontoids suffered a drastic decrease in their diversity, and in the late Miocene the first modern groups appeared in the fossil record (Octodontidae, Abrocomyidae, Eumysopinae, and myocastorids) (Rovereto 1914; Reig 1989; Verzi 1999). A major radiation of other South American rodents also occurred during the middle Miocene (Vucetich *et al.* 1999; Pérez & Vucetich 2011; Arnal 2012). The increase of the hypsodonty observed here in *S. petisensis* relative to other acaremyids was also observed for other caviomorphs [cavioids (Pérez & Vucetich 2011) and dinomyids (Vucetich *et al.* 1999)]. It is supposed to be the consequence of the climatic deterioration in high latitudes of the continent, it means the environment of the southern region of South America changed to a more open environment (grassland-type) due to the increase in aridity, the annual temperature drop (Pascual & Ortiz-Jaureguizar 1990; Ortiz-Jaureguizar & Cladera 2006), and the increase of abrasive materials in the environment (e.g., volcanic ash into the sediments as a product of volcanic activity) (Bellosi 2010). Nevertheless, the involved cavioids and dinomyids are related to modern caviids (Pérez & Vucetich 2011) and dinomyids. That is not the case observed in octodontoids. Phylogenetic results demonstrated that modern octodontids (here represented by *Chasicomys octodontiforme*, *Chasichimys bonaerense*, and *Octomys mimax*) are more closely related with fossil taxa traditionally included into Echimyidae (*Eumysops*, *Stichomys*) than with Acaremyidae. In this context, Acaremyidae would represent an extinct family of octodontoids, endemic from Patagonian South America that lived until, at least, the middle Miocene and left no descendants.

On the other hand, modern Octodontidae have been traditionally hypothesized as having differentiated in high latitudes of the continent, associated with the marked aridization recorded in this region from the middle Miocene (Pascual 1967; Reig 1986; Verzi 1999). This hypothesis assumes the differentiation of Octodontidae from ancestors recorded in high latitudes. In this context, we expect to find Colloncuran and Laventan (middle Miocene) forms with a tooth pattern that pre-announce that of octodontids (teeth with tendency to the euhypsodonty, with metalophulid II reduced or absent, and the tendency to acquire an octodontiform tooth pattern). The phylogenetic results obtained in this work show that *Massoiamys obliquus*, which has lower molars without metalophulid II and with an octodontiform pattern, is the sister group of octodontids. So, it qualifies as morphological ancestor that pre-

announces the octodontiform tooth pattern of octodontids. One of the authors (MEP) is working on a revision of the poorly known genus *Massoiamys*, whose results are relevant to test this hypothesis. Thus, the octodontiform tooth pattern appears at least twice within the superfamily Octodontoidea.

Aknowledgments

References

Ameghino, F. (1887) Enumeración sistemática de las especies de mamíferos fósiles coleccionadas por Carlos Ameghino en los terrenos eocenos de la Patagonia austral. *Boletín del Museo de La Plata*, 1, 1–26.

Ameghino, F. (1889) Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias en Córdoba*, 6, 1–1027.

Ameghino, F. (1891) Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural*, 1, 289–328.

Ameghino, F. (1894) Enumération synoptique des espéces des mammiferes fósiles des formations éocenes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba*, 13, 259–452.

Ameghino, F. (1902) Première contribution à la connaissance de la faune mammalogique des couches à Colpodon. *Boletín de la Academia Nacional de Ciencias de Córdoba*, 17, 71–138.

Arnal, M. (2012) *Sistemática, filogenia e historia evolutiva de roedores Octodontoidea (Caviomorpha, Hystricognathi) del Oligoceno tardío-Mioceno medio vinculados al origen de la familia Octodontidae*. Universidad Nacional de La Plata, La Plata, Argentina, 288 pp.

Bellosi, E.S. (2010) Physical stratigraphy of the Sarmiento Formation (middle Eocene- lower Miocene) at Gran Barranca, central Patagonia. *In*: Madden, R. H., Carlini, A. A., Vucetich, M. G. & Kay, R. F. (Eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change trough the Middle Cenozoic of Patagonia*. Cambridge University Press, Cambridge, UK, pp. 19–31.

Bowdich, T.E. (1821) *An analysis of the natural classifications of Mammalia for the use of students and travelers*. Smith, Paris, 115 pp.

Candela, A.M. & Rasia, L.L. (2011) Tooth morphology of Echimyidae (Rodentia, Caviomorpha): homology assessment, fossils, and evolution. *Zoological Journal of the Linnean Society*, 164, 451–480. http://dx.doi.org/10.1111/j.1096-3642.2011.00762.x

Carvalho, G. & Salles, L. (2004) Relationships among extant and fossil echimyids (Rodentia, Hystricognathi). *Zoological Journal of the Linnean Society*, 142, 445–477. http://dx.doi.org/10.1111/j.1096-3642.2004.00150.x

Ellerman, J.R. (1940) *The Families and Genera of Living Rodents*. British Museum of Natural History, London, 689 pp.

Escapa, I. & Pol, D. (2011) Dealing With Incompleteness: New Advances For The Use Of Fossils In Phylogenetic Analysis. *Palaios*, 26, 121–124. http://dx.doi.org/10.2110/palo.2011.S02

Frailey, C.D. & Campbell, K.E. (2004) Paleogene Rodents from Amazonian Peru: The Santa Rosa Local Fauna. *In*: Campbell, K. E. (Ed.), *The Paleogene Mammalian Fauna of Santa Rosa, Amazonian Peru*. Natural History Museum of Los Angeles County, Los Angeles, pp. 71–130.

Goloboff, P.A., Mattoni, C.I. & Quinteros, A.S. (2006) Continuous characters analyzed as such. *Cladistics*, 22, 589–601. http://dx.doi.org/10.1111/j.1096-0031.2006.00122.x

Goloboff, P.A., Farris, J. S. & Nixon, K. (2008a). A free program for phylogenetic analysis. *Cladistics*, 24, 774–786. http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x

Goloboff, P.A., Farris, J.S. & Nixon, K. (2008b) TNT: Tree Analysis Using New Technology, version 1.1 (Willi Hennig Society

Edition). Program and documentation available at http://www.zmuc.dk/public/phylogeny/tnt.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M. & Szumik, C. (2003) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332. http://dx.doi.org/10.1111/j.1096-0031.2003.tb00376.x

Huchon, D. & Douzery, E.J.P. (2001) From the old World to the New World: a molecular chronicle of the phylogeny and biogeography of Hystricognath rodents. *Molecular Phylogenetics and Evolution*, 20, 238–251. http://dx.doi.org/10.1006/mpev.2001.0961

Kramarz, A.G. (2004) Octodontoids and erethizontoids (Rodentia, Hystricognathi) from the Pinturas Formation, Early–Middle Miocene of Patagonia, Argentina. *Ameghiniana*, 41, 199–216.

Leite, Y.L. & Patton, J.L. (2002) Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. *Molecular Phylogenetics and Evolution*, 25, 455–464. http://dx.doi.org/10.1016/S1055-7903(02)00279-8

Madden, R.H., Guerrero, J., Kay, R.F., Flynn, J.J., Swisher, C.C. & Walton, A.H. (1997) The Laventan Stage and Age. *In*: Kay, R. F., Madden, R. H., Cifelli, R. H. & Flynn, J. J. (Eds.), *Vertebrate Paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington D. C., pp. 499–519.

Mares, M.A. & Ojeda, R.A. (1982) Patterns of diversity and adaptation in South American Hystricognath rodents. *In*: Mares, M. A. & Genoways, H. (Eds.), *Mammalian Biology in South America*. Special Publication Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, pp. 393–432.

Marivaux, L., Vianey-Liaud, M. & Jaeger, J.-J. (2004) High-level phylogeny of early Tertiary rodents: dental evidence. *Zoological Journal of the Linnean Society*, 142, 105–134. http://dx.doi.org/10.1111/j.1096-3642.2004.00131.x

Martin, T. (1992) Schmelzmuster in den Incisiven Alt- und Neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoires Extraordinalles*, 1–168.

Ortiz Jaureguizar, E. & Cladera, G.A. (2006) Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments*, 66, 498–532. http://dx.doi.org/10.1016/j.jaridenv.2006.01.007

Pascual, R. (1967) Los roedores Octodontoidea (Caviomorpha) de la Formación Arroyo Chasicó (Plioceno inferior) de la Provincia de Buenos Aires. *Revista del Museo de La Plata*, 5, 259–282.

Pascual, R. & Ortiz Jaureguizar, E. (1990) Evolving climates and mammal faunas in the Cenozoic South America. *Journal of Human Evolution*, 19, 23–60. http://dx.doi.org/10.1016/0047-2484(90)90011-Y

Patterson, B. & Pascual, R. (1968) New echimyids rodents from the Oligocene of Patagonia and a synopsis of the Family. *Breviora*, 301, 1–14.

Patterson, B. & Wood, A.E. (1982) Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of Museum of Comparative Zoology*, 149, 371–543.

Pérez, M.E. (2010) A new rodent (Cavioidea, Hystricognathi) from the middle Miocene of Patagonia, mandibular homologies, and the origin of the crown group Caviodea sensu stricto. *Journal of Vertebrate Paleontology*, 30, 1848–1859. http://dx.doi.org/10.1080/02724634.2010.522432

Pérez, M.E. & Vucetich, M.G. (2011) A new extinct genus of Cavioidea (Rodentia, Hystricogntahi) from the Miocene of Patagonia (Argentina) and the evolution of cavioid mandibular morphology. *Journal of Mammalian Evolution*, 18 (3), 163–183. http://dx.doi.org/10.1007/s10914-011-9154-1

Pérez, M.E. & Pol, D. (2012) Major radiations in the Evolution of Caviid Rodents: Reconciling Fossils, Ghost Lineages, and Relax Molecular Clocks. *PlosOne*, 7, e48380. http://dx.doi.org/10.1371/journal.pone.0048380

Reig, O.A. (1986) Diversity pattern and differentiation of High Andean rodents. *In*: Vuilleumier F. & Monasterio M. (Eds.), *High Altitude Tropical Biogeography*. Oxford University Press, pp. 404–439.

Reig, O.A. (1989) Karyotypic repatterning as one triggering factor in cases of explosive speciation. *In*: Fontdevila, A. (Ed.), *Evolutionary Biology of Transient Unstable Populations*. Springer-Verlag, Berlin, pp. 246–289. http://dx.doi.org/10.1007/978-3-642-74525-6_15

Rieppel, O. (1994) Homology, topology, and typology: the history of modern debates. *In*: Hall, B. K. (Ed.), *Homology: the hierarchical Basis of Comparative Biology*. Academic Press, San Diego, pp. 55–75.

Rovereto, C. (1914) Los estratos Araucanos y sus fósiles. *Anales del Museo de Historia Natural de Buenos Aires*, 25, 1–250.

Rowe, D.L., Dunn, K.A., Adkins, M. & Honeycutt, R.L. (2010) Molecular clocks keep dispersal hypotheses afloat: evidence for trans-atlantic rafting by rodents. *Journal of Biogeography*, 37, 305–324. http://dx.doi.org/10.1111/j.1365-2699.2009.02190.x

Scott, W.B. (1905) Part III: Glires. *In*: Scott, W. B. (Ed.), *Mammalia of the Santa Cruz beds*. Reports of the Princeton University Expeditions to Patagonia 1896–1899, pp. 384–491.

Simpson, G.G. (1945) The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85, 350 pp.

Tullberg, T. (1899) Über das System der Nagertiere: eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarium Upsaliensis*, 3, 1–514.

Verzi, D.H. (1999) The dental evidence on the differentiation of the ctenomyine rodents (Caviomorpha, Octodontidae, Ctenomyinae). *Acta Theriologica*, 44, 263–282.

Villafañe, A., Pérez, M.E., Abello, A., Bedatou, E. & Bond, M. (2008) Nueva Localidad Fosilífera del Mioceno Medio en el Noroeste de la Provincia del Chubut. *III Congreso Latinoamericano de Paleontología de Vertebrados*, Neuquén, Argentina.

Vucetich, M.G. & Verzi, D.H. (1991) Un nuevo Echimyidae (Rodentia, Hystricognathi) de la Edad Colhuehuapense de Patagonia y consideraciones sobre la sistemática de la familia. *Ameghiniana*, 28, 67–74.

Vucetich, M.G. & Kramarz, G.A. (2003) New Miocene rodents from Patagonia (Argentina) and their bearing on the early radiation of the Octodontoids (Hystricognathi). *Journal of Vertebrate Paleontology*, 23, 435–444. http://dx.doi.org/10.1671/0272-4634(2003)023[0435:NMRFPA]2.0.CO;2

Vucetich, M.G. & Ribeiro, A.M. (2003) A new and primitive rodent from the Tremembé Formation (Late Oligocene) of Brazil, with comments on the morphology of the lower premolars of Caviomorph rodents. *Revista Brasileira de Paleontologia*, 5, 73–82.

Vucetich, M.G. & Vieytes, E.C. (2006) A middle Miocene primitive octodontoid rodent and its bearing on the early evolutionary history of the Octodontoidea. *Palaeontolographica Abteilung*, 277, 81–91.

Vucetich, M.G., Mazzoni, M. & Pardiñas, U. (1993) Los roedores de la Formación Collón Curá (Mioceno medio) y la Ignimbrita Pilcaniyeu, Cañadón del Tordillo, Neuquén. *Ameghiniana*, 30, 361–381.

Vucetich, M.G., Verzi, D.H. & Hartenberger, J.-L. (1999) Review and analysis of the radiation of the South American Hystricognathi (Mammalia, Rodentia). *Comptes Rendus Académie des Sciendes Paris, Sciences de la terre et des planetes*, 329, 763–769.

Vucetich, M.G., Kramarz, A.G. & Candela, A.M. (2010b) Colhuehuapian rodents from Gran Barranca and other Patagonian localities: the state of the art. *In*: Madden, R. H., Carlini, A. A., Vucetich, M. G. & Kay, R. F. (Eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change trough the Middle Cenozoic of Patagonia*. Cambridge University Press, Cambridge, UK, pp. 206–219.

Vucetich, M.G., Vieytes, E.C., Pérez, M.E. & Carlini, A.A. (2010a) The rodents from La Cantera and the early evolution of caviomorph in South America *In*: Madden, R. H., Carlini, A. A., Vucetich, M. G. & Kay, R. F. (Eds.), *The Paleontology of Gran Barranca: Evolution and Environmental Change trough the Middle Cenozoic of Patagonia*. Cambridge University Press, Cambridge, UK, pp. 189–201.

Vucetich, M.G., Verzi, D.H., Deschamps, C.M., Pérez, M.E. & Olivares, A.I. (2011) The evolutionary history of South American Hystricognath rodents. *In*: Rosenberger, A. & Tejedor, M. (Eds.), Origins and Evolution of South American Fossil Mammals. Springer Verlag, New York.

Waterhouse, G. E. (1839) Observations on the Rodentia, with a view to point out the groups, as indicated by the structure of the crania in this order of Mammals. *Magazine of Natural History*, 3, 90–96.

Wible, J.R., Wang, Y., Li, C. & Dawson, M.R. (2005) Cranial anatomy and relationships of a new Ctenodactyloid (Mammalia, Rodentia) from the early Eocene of Hubei province, China. *Annals of Carnegie Museum*, 74, 91–150. http://dx.doi.org/10.2992/0097-4463(2005)74[91:CAAROA]2.0.CO;2

Wood, A. E. (1949) A new Oligocene rodent genus from Patagonia. *American Museum Novitates*, 1435, 1–54.

Wood, A.E. (1955) A revised classification of the rodents. *Journal of Mammalogy*, 36, 165–187. http://dx.doi.org/10.2307/1375874

Wood, A.E. & Patterson, B. (1959) The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bulletin Museum of Comparative Zoology*, 120, 281–428.

Woods, C.A. (1984) Hystricognath rodents. *In*: Anderson, S. & Jones, Jr. J. K. (Eds.), *Orders and Families of recent mammals of the World*. Wiley, Ney York, pp. 389–446.

Woods, C.A. & Howland, E.B. (1979) Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. *Journal of Mammalogy*, 60, 95–116. http://dx.doi.org/10.2307/1379762

APPENDIX 1. Character-taxon matrix used for phylogenetic analysis. Characters in bold represent continuous characters. Characters between brackets represent polymorphic or uncertain scorings. The letter A represent polymorphic scoring [01].

Taxon	Hypsodonty	Character scores (1 … 10 … 20)
Phiomys andrewsi	**0.466**	0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 0 0 0
Deseadomys arambourgi	**?**	1 0 1 0 0 0 1 0 0 0 1 A 0 0 0 0 1 1 0
Plattypitamys brachyodon	**?**	0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 0
Migraveramus beatus	**0.640**	1 0 0 0 ? ? ? 1 1 1 0 1 0 0 0 ? 0 ? 0
Galileomys antelucanus	**0.941**	0 1 0 0 1 A 0 0 0 0 1 0 0 1 0 1 1 1 0
Acaremys murinus	**0.583–0.767**	0 1 0 0 1 A 0 0 0 0 0 1 0 1 0 1 1 1 0
Sciamys principalis	**0.909–1.161**	1 1 0 0 2 1 0 0 0 A 0 1 0 1 0 1 1 1 0
Sciamys petisensis **sp. nov.**	**1.523**	1 1 0 0 ? ? ? ? 0 1 0 1 0 1 0 1 1 ? 0
Protacaremys prior	**0.588**	0 0 0 1 ? ? 1 ? ? ? 1 1 0 0 0 0 0 ? 0
Chasichimys bonaerense	**1.213**	1 1 1 1 ? ? 0 ? ? ? 2 1 1 0 1 ? 2 ? 0
Chasicomys octodontiforme	**?**	1 1 0 1 ? ? 0 ? ? ? 2 1 1 0 1 ? 2 ? 0
Octomys mimax	**?**	1 1 ? 1 ? ? 0 ? ? ? ? 1 1 0 1 1 0 ? 1
Massoiamys obliquus	**?**	1 1 1 1 ? ? ? ? ? ? 2 1 0 0 1 0 2 ? 0
Eumysops laeviplicatus	**1.075**	1 0 0 1 ? ? 0 ? ? ? 2 1 0 0 1 0 2 0 0
Stichomys regularis	**0.681**	1 0 1 1 ? ? 1 ? ? ? 2 1 0 0 0 0 2 1 0

APPENDIX 2. List of characters used in the phylogenetic analysis. An asterisk with the characters signifies some modification to the original character. No name explanation after the character means that it is a new character. The following multistate characters are treated as ordered: 5, and 14.

General dental characters
Hypsodonty (Vucetich & Kramarz 2003)*: treated as a continuous character (see Table 3). The hypsodonty index was measure taking into account crown height (measured at the level of the protoconid) /antero-posterior length of the occlusal surface.
Cusp differentiation (Vucetich & Kramarz 2003): yes (0); no (1). This character is evaluated in juvenile specimens.
Deciduous premolars (Vucetich & Kramarz 2003): normal replacement (0), retention (1). For the living
Octomys mimax we followed Verzi (1994) who proposed that euhypsodont octodontids retain deciduous premolars through life.
Roots: present (0), absent (1).
Upper molariforms
Hypoflexus on P4 (Vucetich & Kramarz 2003)*: absent or incipient (0), poorly developed (1), well developed (2). In cases as in *Platypittamys brachyodon* and *Deseadomys arambourgi* where there is a shallow sink on the lingual border of the tooth, we considered it as character state 0. In other, as in *Galileomys antelucanus* and *Acaremys murinus* where the hypoflexus is present, but less developed than in molars we considered it as character state 1. When the hypoflexus is as developed as in the molars (*Sciamys principalis*) we considered it character state 2.
 Crest number on P4 (Vucetich & Kramarz 2003): three (0), four (1).
Figure-eight-shape dental pattern on M1-M2 (Vucetich & Kramarz 2003)*: absent (0), present (1). Vucetich & Kramarz (2003) do not distinguish between upper and lower figure-eight-shape dental pattern. We divided this character, and differentiate into upper and lower teeth pattern (see character 13).
Metaloph on M1-M3: present and united to the posteroloph (0); present and united to the anterior arm of the hypocone (1).
Quadrangular area of protocone in upper molars (Vucetich & Kramarz 2003): no (0), yes (1).
Lower molariforms
Flexid on the anterior wall of the p4 (Vucetich & Kramarz 2003): present (0), absent (1).
Metalophulid II on p4 (Vucetich & Kramarz 2003)*: short (0), long (1).
Talonid crest of p4 (Vucetich & Kramarz 2003): simple (0), complex (1). It is in reference to the presence or absence of hypolophid.
Figure-eight-shape dental pattern on m1-m2 (Vucetich & Kramarz 2003)*: absent (0), present (1). See explanation of character 7.
Development of metalophulid II on m1-m2 (Vucetich & Kramarz 2003):
 complete (0), variably developed along the tooth row (1), absent (2). The term "metalophulid II" replaces "mesolophid" of Vucetich & Kramarz (2003).
Posterolopid length (Vucetich & Kramarz 2003): short (0), long (1).

Crest obliquity on m1-m3 (Vucetich & Kramarz 2003)*: transversal to the anteroposterior axis of the teeth (0), anterolabially-posterolingually oblique (1). All crests should be oblique to consider character state 1. We take into account only lower molars.

Anteroposterior length of the anterior lobe on m1-m2 respect anteroposterior length of posterior lobe: subequal (0); about 75% (1); less than 50% (2).

Mandibular characters

Discontinuity between the masseteric crest and the fossete for the insertion of the M. masseter medialis pars infraorbitalis (Vucetich & Kramarz 2003): absent (0), present (1).

Anterodorsal limit of the masseteric fossa (Vucetich & Kramarz 2003): absent (0), present (1).

Mental foramen (Vucetich & Kramarz 2003): present (0), absent (1).

Appendix 3. List of unambiguous synapomorphies found in the MPT. Node numbers refer to those given in Figure 5.

Node 1: No synapomorphies
Node 2: Char. 1: 0.588 --> 0.640; Char. 14: 1 --> 0
Node 3: Char. 17: 0 --> 1
Node 4: Char. 10: 1 --> 0
Node 5: Char. 13: 0 --> 1; Char. 5: 0 --> 1; Char. 19: 0 --> 1; Char. 7: 0 --> 1
Node 6: Char. 1: 0.681-0.767 --> 0.941
Node 7: Char. 2: 0 --> 1
Node 8: Char. 2: 0 --> 1;Char. 16: 0 --> 1; Char. 14: 0 --> 1
Node 9: Char. 3: 0 --> 1; Char. 14: 1 --> 2; Char. 17: 1 --> 2
Node 10: Char. 1: 0.681-0.767 --> 1.075; Char. 20: 0 --> 1
Node 11: Char. 13: 0 --> 1
Node 12: Char. 18: 0 --> 1