

A NEW ACAREMYID RODENT (CAVIOMORPHA, OCTODONTOIDEA) FROM SCARRITT POCKET, DESEADAN (LATE OLIGOCENE) OF PATAGONIA (ARGENTINA)

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ABSTRACT—Octodontoidea is the most diverse caviomorph clade presently represented in South America by Octodontidae, Echimyidae, and Abrocomidae. Some evidence suggests that in the past they were taxonomically even more diverse, including several independent lineages with no modern representatives, sometimes considered as families. One of them is Acaremyidae, known until now from the Colhuehuapian–Colloncuran (early to early–middle Miocene) of Patagonia. Here we describe a new octodontoid rodent from the Deseadan (late Oligocene) of Scarritt Pocket (Patagonia): *Changquin woodi*, gen. et sp. nov. Cladistic analysis indicates that the new species is an acaremyid related to the Santacrucian (early Miocene) *Sciomyx*. Acaremyidae was recovered as a monophyletic group. *C. woodi*, gen. et sp. nov., the oldest representative of Acaremyidae, extends the family biochron back to the late Oligocene, and indicates that acaremyids differentiated before the Deseadan. *C. woodi* represents the first Deseadan octodontoid displaying protohypsodont cheek teeth, showing that the Deseadan was a period of important diversification for octodontoids, as it was for the cavioids. *C. woodi* adds a new element to the faunal differences observed between Patagonian and Bolivian Deseadan faunas. A new U-Pb laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) date (27.17 ± 0.54 Ma) for Scarritt Pocket is provided.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Caviomorph rodents, the New World Hystricognathi, are among the most characteristic groups of South American mammals. Recent data demonstrate their presence on the continent since the middle Eocene (Contamana, Peru, Fig. 1A; Antoine et al., 2012). The faunas from Tinguiririca (early Oligocene, Chile, Fig. 1A; Wyss et al., 1993; Flynn et al., 2003; Bertrand et al., 2012), La Cantera (early Oligocene, Argentina, Fig. 1A, B; Vucetich et al., 2010), and Santa Rosa (late Eocene?–Oligocene?, Peru, Fig. 1A; Frailey and Campbell, 2004; Ciancio et al., 2012) show them already differentiated, at least since the early Oligocene, into the four major clades in which caviomorphs have been classically divided: Erethizontoidea (porcupines), Cavoidea (agouties, caviés, capybaras), Chinchilloidea (chinchillas, vizcachas, pacaranas), and Octodontoidea (tuco-tucos, spiny rats, coypus, chinchilla rats). However, their fossil record becomes abundant and diverse only since the Deseadan South American Land Mammal Age (SALMA; late Oligocene); thus, Deseadan caviomorphs are important for understanding of the early evolution of this group of rodents.

Deseadan caviomorphs are known from several localities (Fig. 1A) in Bolivia (Salla and Lacayani; Hoffstetter and Lavocat, 1970; Patterson and Wood, 1982; Lavocat, 1976; Vucetich, 1989), Brazil (Taubaté; Vucetich et al., 1993; Vucetich and Ribeiro, 2003), Uruguay (Nueva Palmira; Kraglievich, 1932; Mones and

Castiglione, 1979), Peru (Moquegua; Shockey et al., 2009), and central Argentina (Corrientes, Mendoza; Gorroño et al., 1979; Bond et al., 1998), but most species and about two-thirds of the genera come from localities in extra-Andean Patagonia (Argentina), especially from the classical localities of Cabeza Blanca (Chubut) and La Flecha (Santa Cruz) (Fig. 1A, B; Loomis, 1914; Wood and Patterson, 1959). Deseadan rodents of Patagonia are quite diverse and most species are endemic, suggesting that these faunas are the result of an early austral radiation in extra-Andean areas, and that this evolution may have occurred in an at least partial isolation from the rest of South America (Aragón et al., 2011).

The relationships among Deseadan rodents, as well as between them and later taxa, are yet poorly understood; revisions with new methods, phylogenetic interest, or evolutionary scope have not been recently performed except for the 'eocardiids,' the basal cavioids. These new analyses of 'eocardiids' show the Deseadan as a period of a very important diversification (Pérez, 2010; Pérez et al., 2010; Pérez and Pol, 2012; Pérez and Vucetich, 2012; Pérez et al., 2012). They strongly suggest that the Deseadan diversity is underestimated, and that new prospecting in classic and new localities, as well as revisions of materials in museums, will reveal that the Deseadan rodent assemblages were richer and more diverse than currently known.

In this paper, we describe a new octodontoid rodent from the Deseadan SALMA, which is also the second rodent species from Scarritt Pocket (Simpson, 1934; Wood, 1949; Chaffee, 1952), a locality in central Patagonia (Figs. 1, 2) that once became very important in the temporal calibration of this SALMA (Marshall et al., 1986; Flynn and Swisher, 1995). This material was found on

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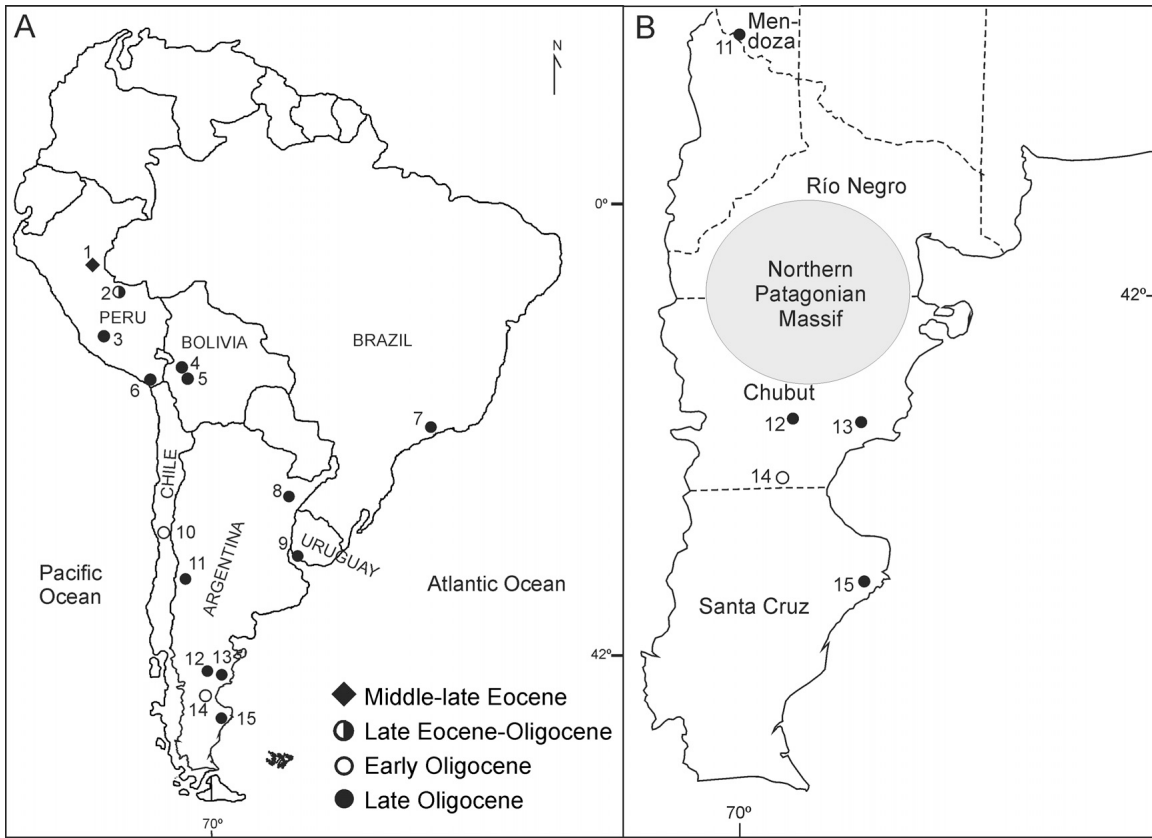


FIGURE 1. Location map with Deseadan localities. **A**, map of South America; **B**, southern Argentina, with details of Patagonia. **1**, Contamana; **2**, Santa Rosa; **3**, Lircay; **4**, Lacayani; **5**, Salla-Luribay; **6**, Moquegua; **7**, Taubaté Basin; **8**, Arroyo Avalos; **9**, Nueva Palmira; **10**, Tinguiririca; **11**, Quebrada Fiera; **12**, Scarritt Pocket; **13**, Cabeza Blanca; **14**, La Cantera, Gran Barranca; **15**, La Flecha.



FIGURE 2. Panorama of the outcrops of Scarritt Pocket. White arrow points to the area where *Changuin woodi*, gen. et sp. nov., was collected. The black arrow shows the ‘crater’ where *Platypittamyx brachyodon* Wood, 1949, and *Scarritia canquelensis* Simpson, 1934, were collected.

the surface by one of the authors (M.R.C.) during field work in 2005.

Besides increasing our knowledge of the rodent diversity for both the Deseadan SALMA in general and Scarritt Pocket in particular, this new taxon allows the exploration of evolutionary trends in the early radiation of octodontoids.

Institutional Abbreviations—MPEF PV, Museo Paleontológico ‘Egidio Feruglio,’ Paleontología Vertebrados, Trelew, Chubut Province, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires Province, Argentina.

Dental Nomenclature—Dental descriptions follow the nomenclature proposed by Candela (1999) and Marivaux et al. (2004).

GEOLOGICAL SETTING AND TIME CALIBRATION

Scarritt Pocket (Figs. 1.11, 2) is one of the most interesting fossil localities discovered by G. G. Simpson during the expeditions to the Argentine Patagonia (Scarritt Expedition of 1933–1934). This is mainly because of the amount, diversity, and good preservation of vertebrate fossils as well as for the absolute dates obtained for several different levels (Marshall et al., 1986).

Scarritt Pocket is on the western side of the Meseta de Canquel, in an engulfment along the flank of the basalt plateau known as the Rinconada de los López or Tapera de López (Simpson, 1934; Chaffee, 1952), about 100 km north-northeast from Sarmiento and 90 km south-southeast from Paso de Indios in central Chubut Province. The Rinconada de los López is one of several similar embayments around the perimeter of the Meseta de Canquel, and similar to those seen around many of the basalt-capped tablelands in central Patagonia. The ‘rinconada’ is a rounded erosional ‘cirque’ where the underlying soft sediments of the Sarmiento Formation have collapsed, bringing down the overlying basalt flows as ‘deslizamientos rotacionales’ (= rotational slumping).

The exposed volcanoclastic sediments are composed of psephitic and pelitic deposits mixed with coarse basaltic materials of local origin and with allochthonous fine pyroclastic materials. These levels have been assigned to the Sarmiento Formation, despite the fact that the abundance of basalts and the composition of their associated deposits are somewhat different from the classic lithologies of this formation (Spalletti and Mazzoni, 1979). The sediments that crop out at Scarritt Pocket are reddish, pinkish, and greenish, distributed in six lithofacies, crossed by and interstratified with basic volcanic rocks (Mazzoni, 1994). The area of the ‘Pocket’ or ‘crater’ (Fig. 2; Marshall et al., 1986:fig. 4) represents a progressive filling of a topographic depression in which the sediments show an apparent synclinal disposition that contrasts with the horizontal disposition of the adjacent sediments (Marshall et al., 1986; Mazzoni, 1994).

The Scarritt Pocket fauna comes from a 9-m-thick portion of the Sarmiento Formation that includes two distinct stratigraphic levels. It includes all fossil vertebrate and plant materials collected from the quarries opened by Simpson (Quarries 1, 2, 3, and 4) and described collectively as Locality I by Marshall et al. (1986). Most of the Scarritt Pocket fauna was collected from the 1-m-thick level at Quarries 1, 2, and 3. The new rodent comes from near the top of Locality I, close to the level of Quarry 4. Our age estimate for the new rodent is based on its stratigraphic occurrence at about the level of Simpson’s Quarry 4. This level is stratigraphically and chronologically related to the level for which we here provide a new U-Pb laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) date (see Supplementary Data 1).

Since the first studies of the faunal association, the assemblage from Locality I has been referred to the Deseadan SALMA, and became important for determining its upper age boundary. The taxonomic assemblage includes the marsupial *Proborhyaena*

gigantea Ameghino, 1897, and the notoungulate *Rhynchippus pumilus* Ameghino, 1897, two taxa known from the classical Deseadan localities La Flecha and Cabeza Blanca (Fig. 1A, B). However, the faunal composition is somewhat different from these two latter, because some seminal and diagnostic Deseadan guide or index taxa, such as *Pyrotherium* Ameghino, 1888, have never been reported from Scarritt Pocket. Moreover, some taxa, such as the rodent *Platypittamys brachyodon* Wood, 1949, and the notoungulate *Scarrittia canquelensis* Simpson, 1934, are only known from this locality despite intensive sampling of many other Deseadan localities. To be sure, other species of *Scarrittia* have been recorded in Deseadan faunas elsewhere (Ubilla et al., 1994; Ribeiro et al., 2010), but *Platypittamys* has never been recorded outside Scarritt Pocket. Hence, this site has been characterized as a local fauna with its own peculiarities. Two other faunas (Localities II and IV of Marshall et al., 1986) occurring at significantly higher topographic levels ‘to the west of Scarritt Pocket’ and ‘from the east rim of Rinconada de los Lopez’ also provided Deseadan mammal species.

Within the 1-m-thick quarry level at Quarries 1, 2, and 3 (Chaffee, 1952; Simpson, field book), many articulated skeletons of *Scarrittia canquelensis* have been discovered and collected ‘from various levels.’ Their co-occurrence at this level with numerous articulated skeletons of small mammals and other vertebrates, together with plant remains and impressions, suggests some kind of a catastrophic event of instantaneous mortality. Plant remains (GGS 158) and impressions (GGS 142) from the ‘crater lake beds’ were mentioned by Chaffee (1952), and a lizard (GGS 150) was mentioned by Marshall et al. (1986). Simpson noted (field book) that the plant remains were most abundant in a tuff lamina that, together with the stratigraphically coincident tuff LGM 83-14, seems to implicate a volcanic eruption event with ash fall as the culprit. LGM 83-14 (Marshall et al., 1986) is a 10–20-cm-thick white fine-grained tuff that gave an imprecise K-Ar age of 23.5 ± 3.6 Ma on plagioclase concentrate. Recently, one of us (R.H.M.) collected a new sample of this tuff, SCARTF, which yielded abundant intact zircon crystals from which 21 of 22 LA-ICPMS analyses found to be equivalent with a weighted mean age of 27.2 ± 0.5 Ma (see Supplementary Data 1–3).

Some authors suggested that two Deseadan faunas could be represented in the beds of Scarritt Pocket, a lower and older Deseadan assemblage from the ‘crater’ or quarry level, and a younger Deseadan in the beds overlying the typical fossiliferous levels (Fig. 2; Wood, 1949; Chaffee, 1952). Later, Marshall et al. (1986) obtained $^{18}\text{K-Ar}$ dates on the basalts of this sequence, which yielded ages between ca. 28 and ca. 21 Ma. By their interpretation, the fossil-bearing levels occur in the interval between 23.4 and 21 Ma. However, Flynn and Swisher (1995) mention without further substantiation that new $^{40}\text{Ar}/^{39}\text{Ar}$ analyses from aliquots of the same sample collected by Marshall et al. (1986), yielded values between 27 and 29 Ma.

Isotopic dates from Scarritt Pocket have been essential for establishing age relationships among Deseadan assemblages from other South American localities (e.g., Salla and Gran Barranca). Although there is still some discussion about the boundaries of the Deseadan SALMA, Dunn et al. (2013) established that the Deseadan encompasses a long interval from 30 to 24 Ma (late early to late Oligocene); thus, a certain degree of diachronism certainly exists among Deseadan local faunas and temporal differences in faunal composition are then expected. Ciancio (2010) proposed that the Deseadan probably includes at least two different temporal intervals, and that the fauna from Scarritt Pocket in particular could belong to the oldest one. The age provided here suggests that at least the quarry level of the Scarritt Pocket fauna represents the early Deseadan in agreement with Wood (1949:45) who stated that “. . .the Scarritt Pocket local fauna is slightly older than the typical Deseadan fauna.” The new fossil rodent comes from a level located somewhat above the level with *Scarrittia* and

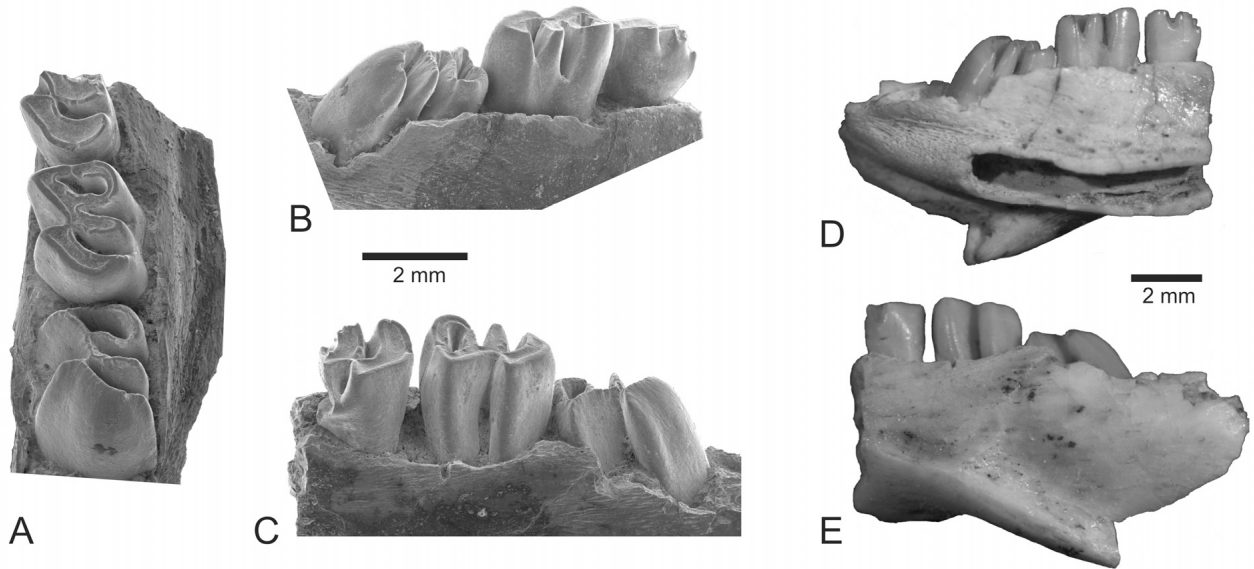


FIGURE 3. *Changquin woodi*, gen. et sp. nov. A–C, detail of dp4–m2; D, E, fragment of left mandible. A, occlusal view; B, D, lingual view; C, E, labial view.

Platypittamys, suggesting that it could be slightly younger than *Platypittamys*.

Paleoclimate inferences from the geology and paleontology of Scarritt Pocket suggest that the sequence was deposited under subhumid conditions, with seasonal rainfall (Mazzoni, 1994). The environment would have been characterized as “. . . forest habitat with plenty of vegetation” (Chaffee, 1952:552) and the presence of low-energy water bodies (Mazzoni, 1994).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Superfamily OCTODONTOIDEA Waterhouse, 1839
Family ACAREMYIDAE Ameghino, 1902
CHANGQUIN, gen. nov.

Etymology—From the Mapuche changquñ = rinconada, in reference to the geographic provenance, Rinconada de los López.

Diagnosis—As for the type and only species.

Distribution—Late Oligocene of Patagonia.

Type Species—*Changquin woodi*, sp. nov.

CHANGQUIN WOODI, sp. nov.
(Fig. 3, Table 1)

Etymology—To Dr. Albert E. Wood, who greatly improved the knowledge of South American Deseadan rodents and described the first rodent species from Scarritt Pocket.

Holotype—MPEF PV 8093. The single specimen known is a left fragmentary mandible of a juvenile without anterior and posterior portions, with the talonid of dp4, m1, and erupting m2.

Occurrence—Scarritt Pocket, Chubut Province. Sarmiento Formation, Mazzoni’s Facies 4 (or 5?) (Mazzoni, 1994:fig. 4a). The fossil was found in the Sarmiento Formation, at the level of Facies 4, not in stratigraphic position. Hence, it could be from higher levels (e.g., Facies 5 or even 6).

Diagnosis—Octodontoid diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): medium-sized octodontoid similar in size to *Sciamys prin-*

cipalis Ameghino, 1887, and *Galileomys antelucanus* Vucetich and Kramarz, 2003; lower cheek teeth protohypsodont (Mones, 1982) and tetralophodont; dp4 with well-developed hypolophid and long posterolophid, both reaching the lingual face of the tooth; m1–2 with cusps completely merged into lophids; metalophulid II long and united to the metalophulid I at the lingual border of m1 and m2 closing the anterofossettid even without wear; metalophulid I with a shallow groove at its midpoint in unworn teeth; and lophids close to each other delimiting narrow fossettid/flexids, but posterolophid not completely fused lingually to the hypolophid in juveniles.

DESCRIPTION

Lower Teeth—The first tooth is more deeply worn than m1 and m2 (Fig. 3A–E), showing that it is a dp4; only the talonid is preserved. The posterolophid is very convex, with its labial end more posteriorly placed than the hypoconid. There is a short anterior arm of the hypoconid that contacts the hypolophid but they are not completely fused. In a juvenile specimen of *Sciamys principalis* (MLP 15-349, Santacrucian SALMA; see Arnal, 2012:155, fig. 4.21) and *Sciamys* sp. from El Petiso (post Colloncuran, early middle Miocene sediments; Patagonia; Arnal and Pérez, 2013), these lophids are united even before m1 has any wear. The hypolophid shows the same anteriorly concave curvature as the posterolophid. A radiograph showed that the posterior root is not reduced yet.

Both m1 and m2 (Fig. 3) are protohypsodont with deep and narrow fossettid and flexids, and cusps merged into the lophids (Fig. 3A). The occlusal surface is slightly terraced, especially after some wear (m1 is more terraced than m2; Fig. 3B). In the unworn m2, the metalophulid I has a central, shallow groove; in the slightly more worn m1, this groove is seen as a contact between lingual and labial portions (Fig. 3A). With a little more wear, both portions would merge, producing a continuous anterior lophid. The second lophid in position is formed by a long posterior arm of the protoconid, posterolingually oriented, and a more labial portion, the metalophulid II, which is transversely oriented. This latter crest is completely merged with the

TABLE 1. Dental measurements (mm) of *Changquin woodi*, gen. et sp. nov.

Dimension	dp4	m1		m2	
AP		2.135	2.50	1.83	2.44
AW		1.586	2.135	1.342	2.135
PW	1.525	1.525	2.135	1.586	2.257

Abbreviations: **AP**, anteroposterior width; **AW**, anterior width; **PW**, posterior width; measurement of dp4 is occlusal; in m1 and m2 left column is occlusal and right column is alveolar.

metaconid, forming a long, continuous ‘U’-shaped lingual crest that also forms the lingual portion of the anterior lophid. Thus, the anterofossettid is formed even without wear, as seen in the erupting m2 (Fig. 3A). The hypolophid is joined to the posterior arm of the protoconid through the ectolophid, and with a little more wear it would merge with the hypoconid in m1. The ectolophid is short in worn m1 and a little longer in the unworn m2. In this latter tooth, the hypolophid is separated from the hypoconid by a small notch. In both m1 and m2, the posterolophid is very convex, although less than in dp4. Lingually, the posteroflexid closes before the mesoflexid (Fig. 3B). This pattern of flexid closure (with the mesoflexid remaining open, whereas antero- and posterofossettids are already formed) will produce, over time, a bilobed figure-8-shaped occlusal pattern, with a large fossettid in each lobe. This pattern is shared with the early to middle Miocene acaremyids (*Acaremys* Ameghino, 1887, *Sciamys* Ameghino, 1887, and *Galileomys* Vucetich and Kramarz, 2003). The hypoflexid is directed slightly backward, and its lingual end faces the metaflexid. It is deeper than the lingual flexids, and its base is hidden by the alveolar border also seen in the little worn m1 (Fig. 3C).

Mandible—Only a small portion of the mandible is preserved (Fig. 3D, E). In this ontogenetic stage, the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle (nMpi) is placed between dp4 and m1, and is posteroventrally inclined about 40° in relation to the alveolar border (Fig. 3E). The nMpi and the anterior portion of the lateral crest sensu Woods (1972) form a half-moon structure with the concavity dorsally oriented. Posteroventrally, the nMpi is continuous with the masseteric crest, which is moderately developed, at a slightly larger angle than the nMpi. In this ontogenetic stage, the end of the alveolus of the incisor is behind and external to the place for the unworn m3.

COMPARISONS

Changquin woodi shares with early to middle Miocene acaremyids (*Acaremys* Ameghino, 1887, *Sciamys*, and *Galileomys*) hypsodont crowns and the temporary figure-8-shaped occlusal pattern. It differs from the above-mentioned acaremyids in the very narrow anterofossettid (metalophulids I and II are much closer to each other than in the other acaremyids), the long metalophulid II united to the metaconid in m2 even without wear (in other acaremyids, the metalophulid II does not reach the lingual wall in m2, or at least it is not merged with the metaconid in an unworn m2, e.g., *Sciamys principalis*), and the relatively shallower anterior portion of the masseteric fossa in the mandible.

Changquin woodi differs from the other Deseadan octodontoids, *Platypittamys brachyodon* Wood, 1949, *Deseadomys arambourgi* Wood and Patterson, 1959, ‘*Deseadomys loomisi*’ Wood and Patterson, 1959, and *Xylechimyis obliquus* Patterson and Pascual, 1968, and the species of *Sallamys* (Hoffstetter and Lavocat, 1970; Vucetich and Ribeiro, 2003; Shockey et al., 2009) in its higher crowns and long metalophulid II. The putative octodontoid *Migraveramus beatus* Patterson and Wood, 1982, differs

from *C. woodi* not only by its low crown and relatively short metalophulid II, but also by the presence of a fifth crest placed between metalophulids I and II, considered a neolophid by most authors (e.g., Patterson and Wood, 1982; Candela et al., 2012).

Several Eocene to early Miocene caviomorphs share with *Changquin woodi* (and the other acaremyids as well) tetralophodont lower cheek teeth with a long metalophulid II, but displaying many variants of this basic morphology. *Prospaniomys* Ameghino, 1902, differs from *C. woodi* in its lower crowns, more oblique lophids, wide flexids/fossettids, and the metalophulid II not joining the metaconid in the m1, at least with little wear. It also differs in the morphology of the mandible with a more horizontal nMpi essentially placed below m1.

Protacaremys Ameghino, 1902, differs in its lower crowns, and wider flexids and fossettids; in the type species *P. prior* Ameghino, 1902, the metalophulid II reaches the metaconid, closing the anterofossettid in very early stages of wear. In the remaining species, the metalophulid II is shorter and does not close the anterofossettid until advanced stages of wear.

Draconomys verai Vucetich et al., 2010, from the early Oligocene of Patagonia differs from *C. woodi* in its very low-crowned cheek teeth, with short metalophulid II, not reaching the external wall of the tooth.

The three middle Eocene caviomorph species recently described, *Canaanimys maquiensis* Antoine et al., 2012, *Cachiyacuy contamanensis* Antoine et al., 2012, and *Cachiyacuy kummeli* Antoine et al., 2012, are similar in general morphology, but more brachydont; the metalophulid II is formed by two portions instead of being complete, and the lophids bear accessory elements.

Most of the species from Santa Rosa have a similar lower molar structure as in *C. woodi*, with four crests basically transversally oriented, and a long metalophulid II that reaches the lingual wall, including *Eobranisamys* Frailey and Campbell, 2004, which is considered a dasyproctine cavioid. They differ from *C. woodi* by being more brachydont and with wider fossettes.

PHYLOGENETIC ANALYSIS

In order to determine the phylogenetic position of *Changquin woodi* within Octodontoidea, a cladistic analysis was performed using a modified version of the data set of Vucetich and Kramarz (2003) with the addition of six taxa and new characters. The matrix includes 20 taxa and 24 morphological characters (see Supplementary Data 2). An equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff et al., 2008a, 2008b), performing a branch-and-bound search algorithm (implicit enumeration in TNT). Four multistate characters (1, 6, 14, and 15) were considered as additive based on the similarity between adjacent character states. 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 BREMER.RUN, and resampling techniques were conducted performing 1000 pseudoreplicates.

The parsimony analysis resulted in a total of 22 most parsimonious trees (MPTs) of 69 steps (consistency index = 0.478, retention index = 0.700). The strict consensus is shown in Figure 4. All of the most parsimonious trees (MPTs) of this analysis placed *Changquin woodi* forming a monophyletic group with *Sciamys principalis* (Fig. 4, node A). Three unambiguous synapomorphies support this clade: (1) protohypsodonty (character 1[2]), (2) molars without cusps differentiable from respective crests (character 2[1]), and (3) metalophulid II in m2 reaching the lingual wall (character 15[0]). This clade is the sister group of *Galileomys antelucanus* (Fig. 4, node B), and is supported by two unambiguous synapomorphies: (1) long metalophulid II in p4, in occlusal view (character 10[1]), and (2) lingual end of metalophulid II in p4 joined to the metaconid (character 11[1]).

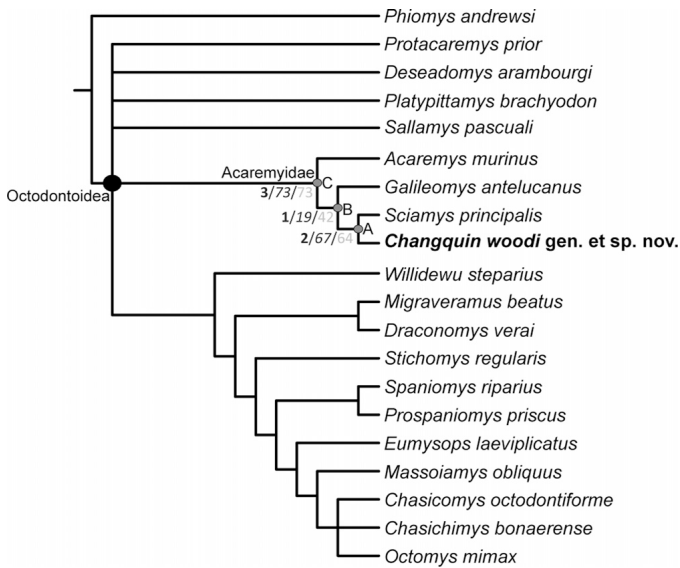


FIGURE 4. Strict consensus of the 22 most parsimonious trees (length = 69; consistency index = 0.478, retention index = 0.700) resulting from cladistic analysis of a modified matrix of Vucetich and Kramarz (2003). The numbers in bold indicate Bremer indices, numbers in italics represent absolute Jackknife values, and numbers in gray represent GC Jackknife values.

Acaremys murinus is the basal most species of Acaremyidae (Fig. 4, node C), and four unambiguous synapomorphies support this clade in all the MPTs: (1) presence of the figure-8-shaped lower cheek teeth (character 3[1]), (2) hypoflexus in the upper premolar poorly developed (character 6[1]), (3) presence of anterodorsal limit of the mandibular masseteric fossa (character 18[1]), and (4) presence of the figure-8-shaped upper cheek teeth (character 20[1]). Moreover, in some MPTs, a fifth unambiguous synapomorphy supports this clade: presence of quadrangular protocone in M1 and M2. Acaremyidae is the node with the highest support values of the analysis (Bremer = 3; jackknife absolute frequency = 73; jackknife GC frequency = 73; see Fig. 4, node C), the clade formed by *Galileomys*, *Sciamys*, and *Changquin* has a low support value (Bremer = 1; jackknife absolute frequency <20; jackknife GC frequency = 42; see Fig. 4, node B), whereas the more derived node of Acaremyidae (i.e., *Changquin* + *Sciamys*) has moderate support values (Bremer = 2; jackknife absolute frequency = 67; jackknife GC frequency = 64; see Fig. 4, node A).

DISCUSSION AND CONCLUSIONS

The superfamily Octodontoidea is the most diverse caviomorph clade, and also the most diverse among the Hystricognathi. Octodontoids are represented in South America by nearly 80 living and extinct genera that have been grouped into three to five major clades, namely the families Echimyidae, Octodontidae, and Abrocomidae plus Ctenomyidae and Myocastoridae (compare McKenna and Bell, 1997, vs. Woods and Kilpatrick, 2005). A recent phylogenetic analysis of the oldest caviomorphs suggests that octodontoids probably differentiated during the middle Eocene (Antoine et al., 2012). However, the early evolutionary and biogeographic histories of octodontoids are far from being understood. Two main evolutionary pathways have been proposed. One hypothesis postulates an early dichotomy between Octodontidae and Echimyidae (e.g., Patterson and Wood, 1982), and that the Oligocene–middle

Miocene octodontoids belong to one of these clades. In this context, acaremyids are considered as a monophyletic clade of Octodontidae (Verzi et al., in press; Vucetich et al., in press). A second hypothesis proposes a more complex octodontoid early history, with different lineages evolving separately (Vucetich and Kramarz, 2003; Vucetich and Vieytes, 2006; Arnal, 2012). In this context, several of the Oligocene–middle Miocene octodontoid genera belong to lineages not closely related to modern representatives (i.e., Echimyidae and Octodontidae). One of these lineages is Acaremyidae. This clade, known for many years only through the Santacrucian (early Miocene) genera *Acaremys* and *Sciamys*, was originally recognized by Ameghino (1902), who related it to porcupines. Later, several authors stated that this group is allied to Octodontoidea, and Wood (1949) incorporated the Deseadan *Platypittamys* as a member of this family (see Vucetich and Kramarz, 2003, for a synthesis of the history of the taxonomy and hypothesis of relationships of Acaremyidae). The present analysis could not resolve the relationships among several of the studied taxa, resulting in a basal polytomy of the octodontoids. However, the acaremyids are recovered as a monophyletic group with relatively high support. In this analysis, *Platypittamys* is excluded from Acaremyidae (although in some of the MPTs it is depicted as sister taxon of this clade), because it is part of the basal polytomy of octodontoids in the strict consensus of the MPTs (Fig. 4). This analysis also differs from Vucetich and Kramarz (2003) in that *Acaremys* was found as the most basal taxon, instead of *Galileomys*. Interestingly, *Changquin* is placed more closely to *Sciamys* (the most derived acaremyid) based on their similar degree of hypsodonty in comparison with the other two acaremyid genera.

Recently, Arnal and Pérez (2013) described a new species of *Sciamys* from the middle Miocene of central Patagonia, which represents the youngest acaremyid known. This record, together with the oldest acaremyid species described here, extends the biochron of the clade by almost 10 Ma, making the *Changquin* lineage 7 Ma older than previously known. The calibration of the phylogenetic tree given the temporal distribution of the acaremyid genera reveals the existence of three ghost lineages extending back to the Deseadan, suggesting that acaremyids must have been more diverse at this time than attested by the fossil record (Fig. 5). The Deseadan was therefore a period of important diversification for the Octodontoids as it was for basal cavioids, and the origin and diversification of Octodontoids occurred prior to the Deseadan SALMA.

In addition, *Changquin* increases the morphological disparity among Deseadan octodontoids because of its degree of hypsodonty. Deseadan octodontoids, both from Patagonia (*Platypittamys* Wood, 1949, *Xylechimyus* Patterson and Pascual, 1968, and *Deseadomys* Wood and Patterson, 1959) and Salla (*Sallamys* Hoffstetter and Lavocat, 1970; *Migraveramus* Patterson and Wood, 1982), are brachydont or display only a very low degree of hypsodonty. This was interpreted as if hypsodonty among octodontoids developed relatively later compared with other caviomorphs. It should be noted that most of the Deseadan species from Patagonia are hypsodont and belong to genera that have been referred to the Chinchilloidea (*Cephalomyopsis* Vucetich, 1985, *Cephalomys* Ameghino, 1897, *Litodontomys* Loomis, 1914, *Eoviscaccia* Vucetich, 1985, and *Scotamys* Loomis, 1914) and Caviioidea (*Asteromys* Ameghino, 1897, and *Chubutomys* Wood and Patterson, 1959). Thus, *Changquin* indicates that at least one lineage within Octodontoidea developed hypsodonty during the Deseadan, paralleling Deseadan chinchilloids and cavioids. In Patagonia, hypsodonty is a precocious and generalized phenomenon that appears in many if not most lineages of Paleogene mammals (e.g., all major clades of xenarthrans, several independent lineages of notoungulates, and even some marsupials). The fossil record shows that this dental trend began very early in Patagonia and that hypsodont mammals became a

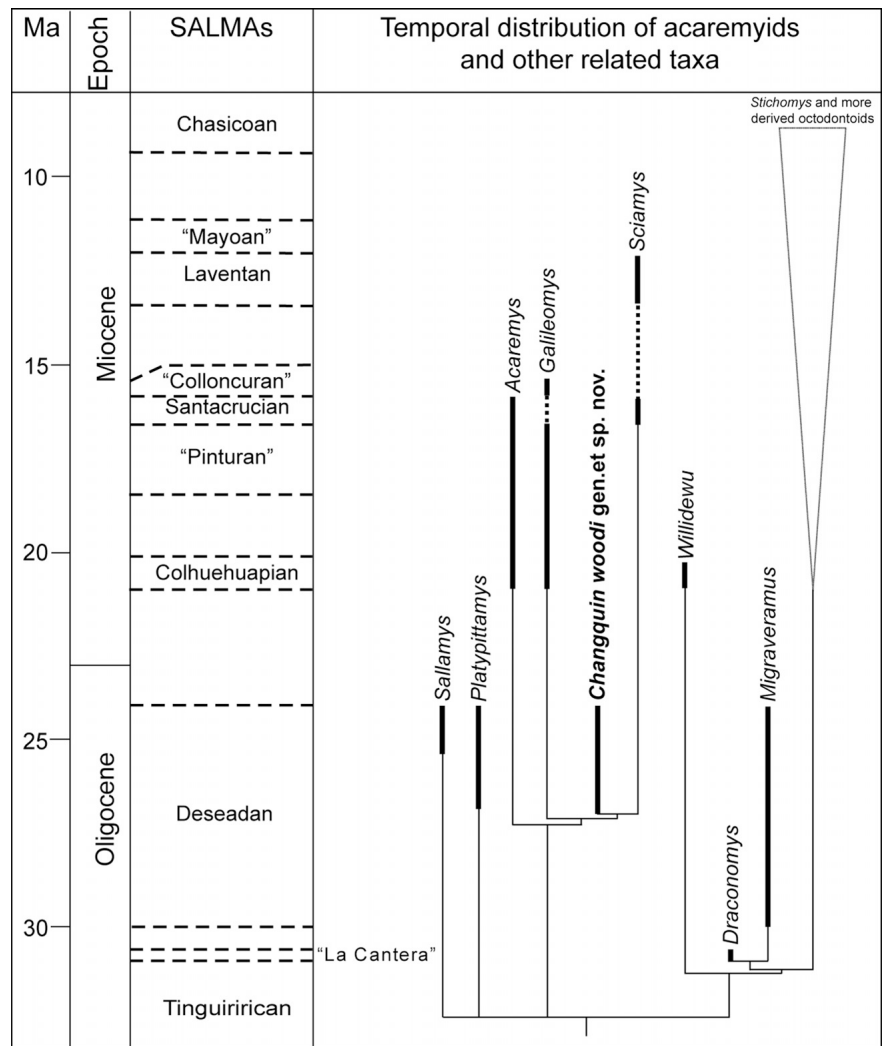


FIGURE 5. Temporal distribution of acaremyids and other related taxa. SALMA calibration is based on Flynn and Swisher (1995), Ré et al. (2010), and Dunn et al. (2013).

dominant component (>50% of taxa) of southern South American faunas after the Eocene–Oligocene boundary, especially among numerous clades of notoungulates (Scarano, 2009; Goin et al., 2012). Different analyses (Reguero et al., 2010; Stromberg et al., 2013) have proposed that hypsodonty in southern South America was a response to dietary grit from labile volcanic ash in soils and soil parent material. Caviomorphs followed this trend and already in the early Oligocene hypsodonty is recorded in rodents from Tinguiririca and La Cantera (Vucetich et al., 2010; Bertrand et al., 2012).

Among Paleogene mammal units, the Deseadan SALMA has the widest latitudinal representation that, although spottily represented, covers a geographic area from about 12°S in Peru to 48°S in Patagonia (see Fig. 1). Deseadan sediments have also been reported from Contamana, but the fauna has not been described yet (Antoine et al., 2012). The distribution of mammal taxa among these localities has raised many interesting questions about biogeography, ecology, and age (e.g., MacFadden, 1990; Vucetich, 1991; Kay et al., 2002; Billet et al., 2008; Ciancio, 2010). Deseadan faunas from Patagonia and Bolivia—especially Salla—are very different in taxonomic composition, particularly at the species level (Table 2). There are also differences between the Bolivian faunas from Salla and Lacayani despite their geographical proximity (Vucetich, 1984; Billet et al., 2008). Among rodents, a single

genus, *Cephalomys*, is shared by Salla and Patagonia, none between Salla and Lacayani, but both genera recorded in Lacayani (*Eoviscaccia* and *Cephalomyopsis*; M. G. Vucetich, unpubl. data) are also present in Cabeza Blanca (Patagonia) and central Argentina (Entre Ríos, Fig. 1A:8), although represented by different species (Table 2). This pattern of distribution is similar to that of the notoungulate *Trachytherus* (Billet et al., 2008), but differs from those presented by other groups of notoungulates (Reguero and Cerdeño, 2005; Reguero et al., 2007) or the cingulata (Ciancio, 2010). Billet et al. (2008:181) proposed that a complex biogeographic pattern combined with temporal discrepancies would explain these differences, and stated that “. . . our understanding of these would increase only with additional temporal data from Patagonian Deseadan localities, and better knowledge of Lacayani fauna.” Also, a better knowledge of the Oligocene diversity in Patagonia and central Argentina (and also Uruguay and Brazil) will help in understanding the Deseadan biogeography, ecology, and the temporal span of the Deseadan SALMA as well as the putative age discrepancies among the different local faunas. *Changquin* adds a new element to these differences among Deseadan faunas, and also reinforces more general disparity between faunas of high and middle latitudes (see Croft et al., 2009), because it is part of a lineage restricted to Patagonia, the acaremyids.

TABLE 2. Rodent species distribution among main Deseadan localities.

Species	Argentina				Bolivia	
	Scarritt Pockett	La Flecha	Cabeza Blanca	Entre Ríos	Lacayani	Salla
<i>Platypittamys brachyodon</i>	x					
<i>Changquin woodi</i> , gen. et sp. nov.	x					
<i>Deseadomys arambourgi</i>		x	x			
' <i>Deseadomys</i> ' <i>loomisi</i>			x			
<i>Scotamys antiquus</i>		x	x			
<i>Litodontomys chubutensis</i>		x	x			
<i>Asteromys punctus</i>			x			
<i>Chubutomys simpsoni</i>		x	x			
<i>Protosteiomys medianus</i>		x	x			
<i>Protosteiomys asmodeophilus</i>		x	x			
<i>Eoviscaccia boliviana</i>					x	
<i>Eoviscaccia australis</i>			x			
<i>Eoviscaccia</i> sp.				x		
* <i>Cephalomyopsis</i> morphotype 2					x	
* <i>Cephalomyopsis</i> morphotype 3			x			
<i>Cephalomyopsis</i> sp.				x		
<i>Incamys bolivianus</i>						x
<i>Migraveramus beatus</i>						x
<i>Sallamys pascuali</i>						x
aff. <i>Neoreomys</i>						x
<i>Branisamys luribayensis</i>						x
<i>Cephalomys arcidens</i>		x	x			
<i>Cephalomys plexus</i>		x	x			
<i>Cephalomys bolivianus</i>						x

*, new combination based on unpublished data of M. G. Vucetich.

Aragón et al. (2011) recently proposed a Patagonian Oligocene scenario that can help explain, at least partially, these differences in taxonomic composition. At this time, northern Patagonia was dominated by a high plateau, the northern Patagonian Massif (NPM; Fig. 1B), about 1200–1500 m high and 100,000 km² in extension, with a humid and seasonally cool climate. This elevation would have acted as a geographic barrier isolating southern and central Patagonia from the rest of the continent. Aragón et al. (2011) stated that the NPM acted also as a selective filter for biotic migrations between both regions. In the particular case of rodents, this barrier/filter could have slowed down the early migration from northern South America—the area where rodents most probably entered South America (Houle, 1998) and where the group first diversified (Frailey et al., 2004; Vucetich et al., 2010; Antoine et al., 2012)—to central and southern Patagonia, and this could explain in part the difference in time between the oldest records of caviomorphs in South America and the oldest one in central Patagonia (Vucetich et al., 2010). The NPM could have also acted as an area of differentiation for caviomorph southern lineages. Understanding the role played by the NPM in the evolution of the Patagonian biota depends on future research including early Cenozoic mammalian faunal diversity and phylogenetic studies of a larger number of taxa.

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