COLHUEHUAPIAN RODENTS FROM GRAN BARRANCA AND OTHER PATAGONIAN LOCALITIES: THE STATE OF THE ART.

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INDEX

ABSTRACT-RESUMEN..... 3

INTRODUCTION…….. 5.

COLHUEHUAPIAN RODENTS AT GRAN BARRANCA……..… 5.

Superfamily Erethizontoidea…….. 6.

Family Erethizontidae……..….. 6.

Superfamily Octodontoidea……...…….. 7.

Family Acaremyidae……..….. 7.

Family Echimyidae……...….. 7.

Superfamily Cavioidea..... 10.

Family Dasyproctidae.....10.

Family Eocardiidae.....11.

Superfamily Chinchilloidea..... 11.

Family Neoepiblemidae.....11.

Family Chinchillidae.....12.

Family Cephalomyidae.....12.

Chinchilloidea incertae sedis.....12.

DISCUSSION..... 13.

Comparison among Colhuehuapian local faunas..... 13.

Evolutionary significance of the Colhuehuapian rodent assemblage...15.

CONCLUSIONS.....19.

REFERENCES..... 21

ABSTRACT

Almost 20 years of fieldwork in the Early Miocene of Patagonia reveals that the various faunas assigned to the Colhuehuapian SALMA share numerous rodent taxa, but they do not share them with faunas of SALMAs immediately younger or older. This supports assignment to a single biochronologic unit. Taxonomical differences especially between the classical localities of Bryn Gwyn and Gran Barranca are scarce and would result mainly from environmental variations. New finds resulted in a dramatic increase of the estimates of diversity for this time, and therefore, the Colhuehuapian caviomorphs currently constitute the most diverse Cenozoic rodent fauna of South America. This high taxonomic diversity could result from the coexistence of old Patagonian lineages together with others of probable northern origin that would have entered Patagonia in a post Deseadan event or events. This diversity also is reflected in various degrees of hypsodonty, an important diversity of occlusal designs and a relatively wide size range, showing that Colhuehuapian caviomorphs had already developed a large variety of adaptive types and strategies in the use of food resources. Colhuehuapian rodent faunas are characterized by the richness of small octodontoids with a mosaic of derived and primitive characters, and the great diversity of erethizontids that have their acme at this time. Most of the Colhuehuapian rodents belong to lineages not recorded in post Middle Miocene faunas; only eocardiids and chinchillids are certainly closely related to extant representatives. After the Colhuehuapian there occurred an impoverishment in taxonomic diversity, variety of occlusal designs, and degree of hypsodonty, suggesting a reduction of adaptive types.

RESUMEN

Casi 20 años de trabajos de campo en el Mioceno temprano de Patagonia revelaron que todas las faunas asignadas a la Edad Colhuehuapense comparten numerosos taxones de roedores no conocidos para las edades inmediatamente más jóvenes o más antiguas, corroborando su asignación a una única unidad biocronológica. Las diferencias taxonómicas, especialmente entre las localidades clásicas de Bryn Gwyn y Gran Barranca, son leves y podrían deberse mayormente a variaciones ambientales. Nuevos hallazgos produjeron un incremento drástico en las estimaciones de diversidad para este lapso y en consecuencia, los caviomorfos colhuehuapenses constituyen actualmente la fauna de

roedores cenozoicos más diversa de América del Sur. Esta alta diversidad taxonómica podría deberse a la coexistencia de linajes patagónicos antiguos con otros de origen septentrional que habrían ingresado a Patagonia durante uno o más eventos post deseadenses. Asimismo, esta diversidad también se refleja en una amplia variedad de grados de hipsodoncia, una importante diversidad de diseños oclusales y un rango relativamente amplio de tamaño que muestra que los caviomorfos colhuehuapenses ya habían desarrollado una gran variedad de tipos adaptativos y de estrategias en el uso de los recursos alimenticios. La fauna de roedores colhuehuapenses se caracteriza por la riqueza de pequeños octodontoideos con un mosaico de caracteres primitivos y derivados, y por la gran diversidad de eretizóntidos que tienen su acmé en este momento. La mayoría de los roedores colhuehuapenses pertenece a linajes no registrados en faunas post Mioceno medio; sólo los eocárdidos y chinchíllidos están estrechamente relacionados con representantes actuales. Luego del Colhuehuapense disminuyen la diversidad taxonómica y la variedad de diseños oclusales y grados de hipsodoncia, sugiriendo una disminución de tipos adaptativos.

INTRODUCTION

The Colhuehuapian South American Land mammal Age (SALMA; Early Miocene) was defined by Simpson (1940) upon the fossil mammal assemblage of Ameghino´s *couches à Colpodon* at central Chubut (Ameghino 1902).

Colhuehuapian rodents, in particular, were first described by Ameghino (1902, 1904) upon materials presumably from the Southern Cliffs of the Colhué Huapi Lake, known worldwide as Gran Barranca (Fig. 1). Ameghino recognized 18 species corresponding to nine genera, grouped in six families. Later, Patterson (1958), Patterson and Pascual (1968), and Vucetich and Kramarz (2003) described a few other species from this locality. Other localities assigned to the Colhuehuapian SALMA (i.e. Bryn Gwyn, Sacanana, Paso Córdova and Cerro Bandera, Fig. 1) have also provided several rodent species (Bordas 1939, Vucetich 1985, Vucetich and Bond 1984, Vucetich and Verzi 1991, 1993, 1996, Vucetich and Kramarz 2003, Candela 2003, Kramarz 1998, 2001a, b, 2005, Pérez et al. 2005), but at present there are no comparative studies of Colhuehuapian rodents as a whole.

During the last 10 years, numerous field projects at Gran Barranca produced one of the most important collections of South American Miocene rodents from a single locality and the efforts on collecting micromammals yielded numerous rare species not previously known from this locality. Thus, these new collections significantly improved our knowledge of the diversity of Colhuehuapian rodents and allowed a more accurate comparison with those of the other mentioned localities. The present knowledge of the rodents from Colhuehuapian levels at Gran Barranca and elsewhere in Patagonia, are here summarized in order to better understand the evolutionary and biogeographic history of the South American Hystricognathi.

Institutional Abbreviations: MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; MLP, Museo de La Plata, La Plata; MPEF, Museo Paleontológico “Egidio Feruglio”, Trelew.

COLHUEHUAPIAN RODENTS AT GRAN BARRANCA

Superfamily Erethizontoidea

Family Erethizontidae. It includes the New World porcupines, medium-sized and heavy-set rodents, mostly with arboreal habits at least in extant species (Woods 1984). Cheek teeth are lophodont and low crowned with characteristic broad enamel covering. Erethizontids at Gran Barranca exhibit an unusual abundance and diversity, both taxonomic and adaptive.

Eosteiromys Ameghino, 1902 has cheek teeth with wide and rather deep fossettes/ids; the uppers have five and the lowers four transverse crests; the incisors are narrow with convex anterior face. *E. segregatus* (Ameghino, 1902) originally referred to the Santacrucian genus *Steiromys* Ameghino, 1887, differs from the type species *E. homogenidens* Ameghino, 1902 (Fig. 2.1) by being smaller and more gracile. A third unnamed species, also smaller than *E. homogenidens*, has hypo- and anteroflexus connected (Candela 2000). This feature is also present in *E. annectens* (Ameghino, 1901) from the "Astrapothericulan" (late Early Miocene; Kramarz 2004), suggesting a close relationship between these species.

Parasteiromys Ameghino, 1904 has pentalophodont upper cheek teeth with a characteristic communication of the hypoflexus and mesoflexus and DP3 during juvenile stages (Candela 1999). *P. friantae* Candela, 1999 differs from the type species *P. uniformis* Ameghino, 1903 in the smaller size, shallower flexi and metaloph isolated from the posteroloph and oriented to the hypocone. According to Candela (1999), *Parasteiromys* is close to the Deseadan *Protosteiromys* Wood and Patterson, 1959 and its molar structure would be the most generalized among the erethizontids.

Hypsosteiromys Patterson, 1958 is the only erethizontid with a clear tendency to hypsodonty (Candela and Vucetich 2002). The upper and lower molars have four oblique crests separated by compressed, deep valleys; the lower molars have a shallow anterior notch isolating the protoconid from the anterolophid; and the incisors are delicate (Patterson 1958). *H. nectus* (Ameghino, 1902) has lower molars with shallower anterior notches, shorter p4, and narrower incisors than the type species *H. axiculus* (Ameghino, 1902) (Fig. 2.2; Candela and Vucetich 2002). This genus would have differentiated early from the remaining extinct porcupines (Candela, 2000).

Branisamyopsis Candela, 2003 is robust with very low crowned cheek teeth. The upper molars are pentalophodont, wider than long, with hypo- and anteroflexus connected.

The lower molars are also pentalophodont and have a well-developed accessory lingual cusp (neoconid) posterior to the metaconid. The p4 has six transverse crests. The mandible is massive, the incisors are wide, and at least the lowers have a planar anterior face (Candela 2003). *Branisamyopsis* would be related to the Deseadan *Eosteiromys* and to the Santacrucian *Steiromys* (Candela 2003). *Branisamyopsis* is represented at Gran Barranca only by the type species *B. australis* Candela, 2003, but congeneric species are recorded in Middle Miocene "Astrapothericulan" and "Colloncuran" deposits (Candela 2003, Kramarz 2004).

Superfamily Octodontoidea

Family Acaremyidae. This group includes Colhuehuapian – "Colloncuran" (Early - Middle Miocene) small-sized rodents with mesodont figure-eight-shaped cheek tooth crowns, and non-molarized P4/4. Vucetich and Kramarz (2003) restricted the concept of Acaremyidae to the genera *Galileomys* Vucetich and Kramarz, 2003, *Acaremys* Ameghino, 1887, and *Sciamys* Ameghino, 1887, excluding the Deseadan *Platypittamys* Wood, 1949. Thus, the family is first recorded in the Colhuehuapian. Acaremyids are represented at Gran Barranca by *Galileomys antelucanus* Vucetich and Kramarz 2003 (Fig. 2.3), with cheek teeth less hypsodont, more cuspidate and terraced than the remaining acaremyids, and by species of *Acaremys* Ameghino, 1887 close to the Santacrucian *A. murinus* Ameghino, 1887 (Vucetich and Kramarz 2003).

Family Echimyidae. It is the most diverse group among Hystricognath rodents (Vucetich and Verzi 1991). Most of the extant echimyids are arboreal or semiarboreal and inhabit intertropical, forested areas (Emmons and Feer 1990, Woods 1984), whereas some species are adapted to more xeric habitats, a few of which are also semifossorial.

Colhuehuapian Echimyidae at Gran Barranca are represented exclusively by Subfamily "Adelphomyinae" (pre Deseadan – Laventan; Early? Oligocene – Middle Miocene). It is characterized by mesodont cheek teeth, without or with slight unilateral hypsodonty, crests tending to become oblique, retention of Dp4/4, shortened lower incisors (Vucetich et al. 1993), and a small mental foramen (Patterson and Pascual 1968, Vucetich et al. 1993).

Prospaniomys Ameghino, 1902 has mesodont and tetralophodont cheek teeth; the uppers with the anteroloph separate from the paracone; the lowers with acuminated labial projections of protocone and hypocone, and meso- and posterolophid transversally shorter than antero- and hypolophid; dp4 with four transverse crests. Only one species, *P. priscus* Ameghino, 1902 (Fig. 2.4), has been named, but some specimens show upper molars with more ephemeral metafossette and more curved anterolingual angle, suggesting they may belong to a distinct species (*Prospaniomys* sp. 1, Fig. 2.5).

Protacaremys Ameghino, 1902 is smaller and higher crowned, with more oblique crests, and dp4 with five transverse crests. The type species *P. prior* Ameghino, 1902 (Fig.2.6) differs from *P. avunculus* Ameghino, 1902 (Fig. 2.7) by being rather larger and having a less prominent mandibular masseteric crest. A fragmentary right mandible with m1-2 more quadrangular (Fig. 2.8) represents a new species tentatively referred to this genus. Another species, "*P.*" *pulchellus* Ameghino, 1902, is transferred in this paper to the genus *Acarechimys* (see below).

The monotypic genus *Paradelphomys* Patterson and Pascual, 1968, only known through the type specimen of *P. fissus* Patterson and Pascual, 1968, differs by the absence of mesolophid, much more oblique crests, and hypoconid isolated from the hypolophid. Currently this specimen is missing.

Octodontoidea incertae sedis. Here we note those basal octodontoids with uncertain affinities (Vucetich and Kramarz 2003, Vucetich and Vieytes 2006), previously referred to Octodontidae or Echimyidae.

Acarechimys Patterson, 1965 (in Kraglievich. 1965) includes one of the smallest hystricognath rodents so far known. Cheek teeth are brachyodont. Lower molars have three main transverse crest separated by broad and shallow lingual flexids which turn into fossettids early in wear. The upper molars have four transverse crests; the anterior and posterior labial flexi become fossettes early in wear. Deciduous premolars are retained throughout life, as in the Adelphomyinae and modern octodontoids. The dp4 has a wide and subcircular anterior basin, usually opened on the labial side. This genus has a wide temporal range, from Colhuehuapian (Vucetich et al. 1993) up to Laventan (Walton 1997) SALMAs. The three recognized species were found in Santacrucian localities. To date,

materials of this genus from other SALMAs could not be assigned at the species level. *Acarechimys* is represented at Gran Barranca by three isolated cheek teeth (Fig. 2.9) similar in size to *A. minutissimus* (Ameghino, 1887).

Acarechimys pulchellus comb. nov. (Fig. 2.10a-b), is a rare species. It differs from the species of *Protacaremys* in having cheek teeth with less columnar appearance, much shorter trigonid, broader and less oblique crests separated by shallower flexids that turn into enamel lakes early in wear, and reduced mesolophid in m2 – m3. These dental characters are diagnostic features of *Acarechimys*, and it is herein transferred to this genus. It is slightly larger than *A. minutus* (Ameghino, 1887).

The minute *Caviocricetus* Vucetich and Verzi, 1996 (Fig. 2.11) has very low-crowned and strongly terraced cheek teeth, an extreme condition unknown among the other Hystricognathi (Vucetich and Verzi 1996). The dp4 has a characteristic V-shaped anterior border. The lower molars have three transverse crests separated by very shallow and wide labial flexids, which do not become enamel lakes with wear. A low, independent knob is present in the anterolingual flexid. The upper molars are longer than wide, with four transverse crests; the antero- and mesoloph are shorter than the remaining crests.

A still unnamed genus and species nov. (Fig. 2.12) is a small octodontoid with low-crowned and slightly terraced cheek teeth occurring both at Gran Barranca and Bryn Gwyn. The dp4 is structurally similar to *Acarechimys*, but differs from the latter in that m1-2 have four transverse crests, the meso- and posterolophid are shorter than the remaining lophids, and the lingual portion of the mesolophid curves forward and reaches the posterolabial slope of the metaconid, resembling the condition observed in *Platypittamys* and *Galileomys* (Vucetich and Kramarz 2003). The m3 is trilophodont while all the upper cheek teeth are tetralophodont. Differences in size suggest the distinction of two species, only the largest of which occurs at Gran Barranca.

Protadelphomys Ameghino, 1902 has a peculiar systematic history (Ameghino 1902, Vucetich and Bond 1984, Vucetich et al. 1992, Vucetich and Verzi 1994). *P. latus*, the single nominated species of this genus, was described upon a mandibular ramus with p4-m3 of uncertain provenance (Ameghino 1902); currently it has only the m3. *Protadelphomys* is very common in Bryn Gwyn, but very rare in Gran Barranca. In this paper we differentiate the more delicate population of Gran Barranca as *P. latus*

morphotype A (Fig. 2.13), from the largest one of Bryn Gwyn (and Sacanana) as *P. latus* morphotype B, probably representing two different species. The single tooth (m3) preserved in the holotype of *P. latus* Ameghino, 1902 provides too few characters to elucidate to which morphotype it belongs. *Protadelphomys* has mesodont cheek teeth, the uppers with conspicuous unilateral hypsodonty with broad and slightly oblique crests separated by a narrow valley. Upper molars have four crests, but the hypoflexus is connected to the anterolabial valleys, which in turn closes labially early in wear, the lingual end of the mesoloph is curved backward merging with the posteroloph, and it is isolated from the hypocone; the mesofossette is very ephemeral. This arrangement produces a characteristic transitory S- shaped occlusal pattern. The lower molars are three-crested; the hypoflexid is continuous with the posterolingual flexid. The DP3 is present during juvenile stages. In contrast to younger octodontoids and contemporaneous "Adelphomyines", this genus exhibits normal replacement of the deciduous dentition; both upper and lower permanent premolars are simpler than molars. The incisors are very broad and long, the lowers with a flat anterior face, the uppers are strongly curved and have a conspicuous longitudinal crest on the anterior face. *Protadelphomys* is closely related to the Colhuehapian *Willidewu* Vucetich and Verzi, 1991 and the Deseadan *Sallamys* Hoffstetter and Lavocat, 1970 (Vucetich and Verzi 1991).

Superfamily Cavioidea

Family Dasyproctidae. It includes large to middle sized cursorial rodents. Modern species inhabit the lower strata of the intertropical-forested areas (Emmons and Feer 1990). All of them have hypsodont tetra- or pentalophodont cheek teeth with a strong tendency to retain a complex occlusal pattern throughout their ontogeny, by virtue of the persistence of fossettes and fossettids, which are very compressed. Patagonian dasyproctids belong to an austral radiation of the family not related to the extant species (Vucetich 1984, Vucetich and Verzi 1994, Kramarz 1998). The only record of this family in Gran Barranca is an isolated hypsodont and pentalophodont upper molar (MACN A 52-163, Fig. 3.1a-b) interpreted by Wood and Patterson (1959) as a dasyproctid allied to *Neoreomys* Ameghino, 1887. However, this molar differs from *Neoreomys* in its wider fossettes and acuminated lingual apices, suggesting that relationship with this genus is not very close (Kramarz 1998).

Family Eocardiidae. It includes several small to middle sized hystricognath rodents with bi-prismatic meso- to euhypsodont cheek teeth. The family has traditionally been considered as the Oligocene – Miocene ancestral group of the modern caviids (Ameghino 1898, Scott 1905, Kraglievich 1934, 1940, Landry 1957). Eocardiids are represented in Gran Barranca only by *Luantus initialis* Ameghino, 1901 (Fig. 3.2), with lower crowned cheek teeth and less molarized p4 than the type species *L. propheticus* Ameghino, 1899 ("Astrapothericulan").

Superfamily Chinchilloidea

Family Neoepiblemidae. This family typically includes large to giant Late Miocene rodents characterized by euhypsodont multilaminar cheek teeth with thick interlaminar layers of cement. The only representative of this group in Gran Barranca is *Perimys* Ameghino, 1887. Besides its smaller size, it differs from *Neoepiblema* Ameghino, 1889 and *Phoberomys* Kraglievich, 1926 by its bilaminate cheek teeth (except M3 that is trilaminate), and the morphology of the P4 that opens on the labial side, in contrast to the upper molars. This genus is also recorded in the Santacrucian SALMA, although by different species. *Perimys* would be close to the Deseadan *Scotamys* Loomis, 1914.

Ameghino (1902) described four species for Gran Barranca. *Perimys incavatus* Ameghino, 1902 (Fig. 3.3) is slightly smaller than the living plain viscaccia, and differs from the Santacrucian species by having cheek teeth with broader and more rounded laminae, and upper molars lacking labial enamel cover and labial flexus. *P. transversus* Ameghino, 1902 is only known through the type specimen, similar in size to the type of *P. incavatus*, but the lower cheek teeth are more quadrangular, and the laminae are less oblique; these could be synonyms. *P. dissimilis* Ameghino, 1902 (Fig. 3.4) is much smaller than the other two; the lower cheek teeth have more delicate and strongly curved laminae, and very conspicuous lingual flexids. The upper molars have also thin laminae and the labial walls have a vertical enamel band between two labial flexi. This species differs from all the remaining species of *Perimys* by having an anterior projection of the labial end of the posterior lamina in the lower molars and a posterior projection of the lingual end of the anterior lamina in the uppers. "*P. incurvus"* Ameghino, 1902, is only known through the type specimen, which at present is missing from the MACN collections. According to

Ameghino (1902), this species is even smaller than *P. dissimilis*, the laminae are also much curved, and the p4 is reduced. These features suggest that "*P. incurvus*" was based on a juvenile of *P. dissimilis*. Some specimens from Gran Barranca have cheek teeth similar in morphology to those of *P. incavatus* but they are even smaller than juveniles of the latter; they could belong to a still unnamed species.

Family Chinchillidae. This family includes rather delicate rabbit-like rodents (Woods, 1984) with proto- to euhypsodont bi- or trilaminar cheek teeth. There are only three extant genera grouped in two subfamilies: Lagostominae (*Lagostomus*) and Chinchillinae (*Chinchilla* and *Lagidium*). The fossil record is almost entirely restricted to the Lagostominae (but see Croft et al. 2004), characterized by bilaminar cheek teeth (except M3). The family is represented at Gran Barranca only by three isolated cheek teeth referable to *Eoviscacia australis* Vucetich, 1989 (Fig. 3.5-6), originally described for the Deseadan. This species has more hypsodont cheek teeth than *E. boliviana* Vucetich, 1989 (Deseadan of Bolivia); it differs from the species of *Prolagostomus* Ameghino, 1887 and *Pliolagostomus* Ameghino, 1887 (Santacrucian – "Colloncuran"), by its broader and less penetrating hypoflexus/-id, more persistent fossettes/tids, and less developed posterior lobe in the M3.

Family Cephalomyidae. It includes extinct rodents with different degrees of hypsodonty, characterized by an asymmetric dental pattern (i.e. the occlusal pattern of the lower cheek teeth does not mirror that of the uppers), probably of Chinchilloid affinities (Vucetich 1985, 1989; Kramarz 2001b, 2005). Cephalomyids are diverse and very well represented in other Colhuehuapian local faunas, but at present they are known in Colhuehuapian levels of Gran Barranca only through an isolated mesodont, rooted, bilobed upper cheek tooth, similar to the DP4 of *Soriamys* Kramarz, 2001b (Fig. 3.7).

Chinchilloidea incertae sedis. A genus and species of uncertain position within the superfamily is represented at Gran Barranca by an upper protohypsodont cheek tooth, with three small roots (Fig. 3.8). An extended hypoflexus divides the occlusal surface into an

anterior laminar lobe and a subtrapezoidal posterior one. This posterior lobe has a short and shallow flexus open to the labial wall.

DISCUSSION

Comparison among Colhuehuapian local faunas and paleoenvironmental inference

Sensu stricto, the Colhuehuapian is defined by the fauna of Gran Barranca. Other local faunas from central and northern Patagonia (i.e. Bryn Gwyn, Cerro Banderas, Sacanana, Paso Córdova; Fig. 1) were assigned to this SALMA based upon mammals other than rodents. Collections made during the last 20 years in these localities permit the first analysis of the diversity of the rodents of this interval. Other faunas out of Argentina have also been assigned to the Colhuehuapian (e.g. Flynn et al. 1995), but rodents have not been reported, or they have not been adequately described yet.

Among Colhuehuapian faunas, the rodent assemblage at Gran Barranca is the best known; with at least 18 genera it is the most diverse rodent fauna for a single locality. The stratigraphic section bearing Colhuehuapian fauna (=Lower Fossil Zone, Madden et al. this book, Fig…) is about 40 meters thick and spans about 0,6Ma (Madden et al. this book, Bellosi this book); 12 of these genera (*Eosteiromys*, *Hypsosteiromys*, *Branisamyopsis*, *Galileomys*, *Acarechimys*, *Prospaniomys*, *Protacaremys*, *Acarechimys*, *Caviocricetus*, Octodontoidea gen. et sp. nov. *Luantus* and *Perimys*) are represented together in one of the levels more intensively worked with different collecting techniques (level B, in Madden et al. this book, FigXX.). Until now the richest caviomorph fossil assemblage was that of La Venta (Middle Miocene, Colombia) with 13 genera, 12 of which are represented in the richest level (Walton, 1997).

In Gran Barranca the rodent assemblage is dominated by brachy- or mesodont octodontoids, comprising nine genera, which represent 50% of the total generic diversity. The erethizontids, with four genera (including eight species) achieved here their greatest diversity, representing 22% of the total diversity. Thus, the rodent assemblage at Gran Barranca is dominated by low-crowned species, suggesting varied forested environments. Morphofunctional studies showed that at least some Miocene erethizontids of Patagonia would have had climbing and grasping abilities, which are in agreement with the presence of forested habitats (Candela *et al*. in press). Neither evolutionary trends, nor the prevalence

of a special adaptive type in any level could be seen along the stratigraphic sequence, suggesting relative environmental stability during its deposition. This stability is also suggested by the record of several genera (*Hypsosteiromys*, *Protacaremys*, *Prospaniomys* and *Perimys*) throughout the Lower Fossil Zone.

Among euhypsodont genera, *Perimys* is largely the most abundant and diverse. Although euhypsodont species are generally associated with open environments, *Perimys* could indicate water bodies, as the giant neoepiblemids of the Late Miocene do. These latter, sharing with *Perimys* the basic gross dental morphology (laminar cheek teeth with a thick cement interlaminar layer and a thin enamel surrounding layer), are always recorded in fluvial sediments. Sedimentological evidence (Bellosi, this book) also suggests a fluvial depositional setting for the Colhuehuapian levels at Gran Barranca. The remaining high-crowned taxa (*Eoviscacia australis*, *Luantus initialis*, Chinchilloidea *i.s.*, Cephalomyidae? indet., and *Soriamys* sp.) are very rare and would be the only indicators of open environments, probably marginal.

The best-known Colhuehuapian fauna outside Gran Barranca is that of Bryn Gwyn, but taxa are fewer than in Gran Barranca (Tb. 1). Although most genera were found in both localities, *Willidewu* (Octodontoidea), *Cephalomyiopsis* (Cephalomyidae) and *Australoprocta* (Dasyproctidae) are recorded in Bryn Gwyn but not in Gran Barranca. Given the large number of rodents found in Gran Barranca (within this project alone, almost 400 specimens were collected) and the variety of collecting techniques used, we think that the lack of records reflects actual absence. Among the taxa not recorded in Bryn Gwyn, *Protacaremys* is important because of its abundance in Gran Barranca. On the other hand, the frequencies of shared taxa are quite different: *Eoviscaccia*, *Protadelphomys*, *Caviocricetus* and Octodontoidea gen. et sp. nov. are abundant in Bryn Gwyn, but very scanty in Gran Barranca. Another important difference is the much greater diversity achieved by erethizontids in Gran Barranca, whereas cephalomyids are much better represented in Bryn Gwyn. Consequently, the proportion of hypsodont rodents is higher in Bryn Gwyn than in Gran Barranca. These differences in composition show that, unlike in Gran Barranca, the open environments would have prevailed in Bryn Gwyn. Sedimentological and paleopaedological data agree with this interpretation (Bellosi this book, Bellosi and González this book).

Some authors (Simpson 1940) suggested these two faunas are slightly diachronic, that of Bryn Gwyn being somewhat younger, and recommended to distinguish it as "Trelewense" (Kraglievich 1930). The record in Bryn Gwyn of one species of *Luantus* more derived than *L. initialis* of Gran Barranca would be in agreement with this hypothesis (Pérez et al. 2005). However, our comparison of both rodent assemblages shows they are very similar, sharing several taxa even at the species level. Moreover, most of the shared genera are not known for other SALMAs. Consequently, the rodents as a whole do not support the hypothesis of temporal difference between the faunas to justify separating them in two different biochronological units. On the contrary the compositional differences above mentioned seem to be mostly the result of environmental differences. If any, temporal differences would be little.

The local faunas of Paso Córdova, Sacanana and Cerro Banderas, as well as their respective environmental conditions are still too poorly known to permit an accurate analysis. With the exception of *Banderomys*, which is exclusive from Cerro Bandera, all the recorded genera occur also in Bryn Gwyn, but two of them are not in Gran Barranca, for which their composition is more similar to that of Bryn Gwyn than Gran Barranca (Tb. 1).

Among the exclusive Colhuehuapian rodent taxa, *Caviocricetus lucasi* has the widest areal distribution, as it is recorded in four of the five local faunas; eventually it may be used as a guide taxon of this SALMA.

Evolutionary significance of the Colhuehuapian rodent assemblage.

The family composition of the entire Colhuehuapian rodent assemblage is similar to that of the other Late Oligocene - Middle Miocene Patagonian faunas, as it includes families that are currently restricted to the Brazilian Subregion (sensu Hershkovitz 1958, Erethizontidae, Echimyidae, and Dasyproctidae), others constrained to the Patagonian Subregion (Chinchillidae), the primitive caviids traditionally grouped in the Eocardiidae, and several extinct ones, such as the Acaremyidae (not recorded in the Late Oligocene Deseadan yet), Cephalomyidae and Neoepiblemidae. In fact, taking into account mammal family composition, the Colhuehuapian SALMA has been long considered as part of a major faunistic unit (Pansantacrucian Cycle; Pascual et al. 1996 and references therein).

On the contrary, the generic composition (Tb. 1) is very characteristic, especially because of the great diversity and abundance of small octodontoids, and the diversity of erethizontids and cephalomyids. Thirteen of the 23 rodent genera are exclusive of this period (Tb. 1), and notably three of them (*Hypsosteiromys*, *Caviocricetus* and *Soriamys*) represent a particular lineages only recorded during this period up to now.

The octodontoids, with ten genera belonging to several lineages, are the most enigmatic and interesting group of this period. Oligocene – Middle Miocene octodontoids have been referred traditionally to Octodontidae or Echimyidae (see Patterson and Wood 1982). Modern Echimyidae and Octodontidae, as well as the remaining extant octodontoids, share the retention of Dp4/4 and an incisor enamel microstructure with rectangular interprismatic matrix in multiserial Hunter-Schreger bands (Martin 2005). However, half of the Colhuehuapian octodontoid genera (*Caviocricetus*, the clade *Protadelphomys-Willidewu*, and the acaremyids *Galileomys* and *Acaremys*) display different combinations of "primitive" and "derived" states of these characters, therefore they cannot be easily classified within the modern groups. We consider that the early evolution of the octodontoids was more complex than the simple dichotomy Octodontidae-Echimyidae previously proposed, and that these taxa represent different branches of the early radiation of the Octodontoidea (Vucetich and Kramarz 2003, Vucetich and Vieytes 2006).

Acarechimys has alternatively been classified within the Echimyidae or Octodontidae (Patterson and Wood 1982, Vucetich and Verzi 1991, Vucetich et al. 1993, Walton 1997, Verzi 2002, Carvalho and Salles 2004). At present there is no strong evidence supporting either one or the other hypothesis. *Acarechimys* still retains a very primitive dental morphology, but it has the derived characters of modern octodontoid families mentioned above, suggesting it would be close to the differentiation of Echimyidae and Octodontidae.

Among Colhuehuapian octodontoids, the Adelphomyines are the closest to the modern Echimyidae. At least three different lineages can be identified among genera traditionally included in this subfamily: 1) *Prospaniomys-Spaniomys* (Santacrucian)-*Maruchito* ("Colloncuran", Ameghino 1902, Vucetich et al. 1993); the extant genus *Callistomys*, usually considered an Echimyinae, was proposed as a survivor of this lineage

(Emmons and Vucetich 1998); 2) *Protacaremys-Prostichomys* ("Astrapothericulan")-*Stichomys* and *Adelphomys* (Santacrucian; Kramarz 2001c); and 3) *Xylechimys* (Deseadan)-*Paradelphomys-Ricardomys* (Laventan)- *Olallamys* (extant, Dactylomyinae; Patterson and Pascual 1968, Walton 1997, Carvalho and Salles 2004); *Eodelphomys* (pre Deseadan, Santa Rosa, Peru, Frailey and Campbell 2004), could be related to this lineage. All these proposals have to be tested within a broader systematic context; thus we provisionally accept the subfamily "Adelphomyinae" as a non-monophyletic group (Vucetich and Verzi 1991, Carvalho and Salles 2004).

On the contrary, it is clear that Colhuehuapian erethizontids are not closely related to the extant species (mostly restricted to the Brazilian Subregion). They belong to a Patagonian clade differentiated from modern representatives at least by Late Oligocene (Candela, 2003; Candela and Morrone, 2003). It is only through the great taxonomic and adaptive diversity achieved by Colhuehuapian erethizontids (especially recorded in Gran Barranca) that the magnitude of this southern radiation is manifested.

Among hypsodont rodents, cephalomyids have their acme and are the most diversified group during this SALMA (Kramarz 2001b, 2005). Two well-differentiated lineages are recognized; one is represented by the euhypsodont *Cephalomyiopsis* Vucetich, 1985 with simplified figure-eight lower molar pattern (maybe related to the Deseadan *Cephalomys* Ameghino, 1897 and *Litodontomys* Loomis, 1914) and the other by the protohypsodont *Soriamys* with trilaminar lower molar pattern. Both lines would have radiated in pre-Deseadan times from an ancestor with a dentition very close to that of *Banderomys* (Kramarz, 2005). Except for the record of a cephalomyid close to the *Cephalomys* from the middle Miocene Quebrada Honda Group (Bolivia; Frailey, 1980), this family is not represented in other faunas younger than Colhuehuapian.

Contrarily, Colhuehuapian eocardiids and chinchillids are less diversified than cephalomyids. The eocardiid *Luantus initialis* is structurally ancestral to euhypsodont Santacrucian eocardiids (Kramarz, 2006), which in turn are the ancestral stock of the modern caviids (Ameghino, 1898; Scott, 1905; Kraglievich, 1934, 1940; Landry, 1957). The chinchillid *Eoviscacia australis* is structurally the ancestor of *Prolagostomus* and *Pliolagostomus* (Santacrucian – "Colloncuran"), which are closely related to the extant lagostomines (Chinchillinae probably have an extraPatagonian origin, Croft et al. 2004).

Several genera of the entire Colhuehuapian rodent assemblage belong to lineages already represented in Deseadan faunas of Patagonia, although mostly by different genera, v.gr. Eocardiidae (*Asteromys-Luantus*), Chinchillidae Lagostominae (*Eoviscaccia*), Cephalomyidae (*Cephalomyiopsis*), Neoepiblemidae (*Scotamys-Perimys*), Echimyidae Adelphomyinae (*Xylechimys-Paradelphomys*), Erethizontidae (*Protosteiromys-Eosteiromys*). However, others have no known ancestors in Patagonia: *Caviocricetus*, *Protadelphomys - Willidewu,* Acaremyidae, Octodontoidea Gen. et sp. nov., and *Hypsosteiromys*. At least one of these lineages, the clade *Protadelphomys - Willidewu* (Vucetich and Verzi 1991) is already represented in the Deseadan of lower latitudes (*Sallamys*). Consequently, the high diversity of Colhuehuapian rodents could result from the coexistence of Patagonian lineages together with others that entered in post-Deseadan times. Based on palynological data, Barreda and Palazzesi (2007, this book) stated that Early Miocene climate allowed the southward dispersion of Neotropical elements. However, the validity of this hypothesis has to be tested after more intensive prospecting of Deseadan levels of Patagonia, which have not been worked as intensively as those with Colhuehuapian faunas.

After the Colhuehuapian a decrease of taxonomic diversity, variety of occlusal designs and hypsodonty degrees, suggests an impoverishment of adaptive types. This is especially notable for the Santacrucian, known mainly from the southern end of Patagonia, during which the prevailing taxa were proto- and euhypsodont ones. This could be the result of a progressive climatic deterioration in Patagonia during the Early – Middle Miocene (Barreda and Palazzesi 2007, this book). But it is also possible that these differences are magnified by the latitudinal differences between Colhuehuapian and Santacrucian localities (Fig. 1). In fact, “Colloncuran” faunas from northwestern Patagonia (Fig. 1), somewhat younger than Santacrucian, show slightly higher diversity of brachyodont forms than the Santacrucian ones (Vucetich et al. 1993, and unpublished personal data).

CONCLUSIONS

The efforts of fieldwork in the Early Miocene of Patagonia during the last twenty, and especially the last ten years in Gran Barranca, provide a more integrative knowledge of the caviomorph evolution and diversity during this interval. The new findings reveal that all the faunas assigned to the Colhuehuapian SALMA share numerous rodent taxa, not known for faunas assigned to immediately younger or older SALMAs, which supports their assignment to a single biochronologic unit. Despite the faunas from northern Patagonia being more similar to that of Bryn Gwyn than to that of Gran Barranca, the taxonomical differences are scarce and could result mainly from environmental variations.

These new finds resulted in a dramatic increase of the diversity known for this time. Numerous new taxa (not named yet) are here described, and several others are first mentioned for Gran Barranca. Therefore, Colhuehuapian caviomorphs are currently the most diverse Cenozoic rodent fauna of South America. This high taxonomic diversity would result from the coexistence of old Patagonian lineages together with others of probable northern origin that would have entered Patagonia in one or more post Deseadan event. This diversity is also reflected in a wide range of observed hypsodonty, an important diversity of occlusal designs (cuspidate, terraced, laminar, sigmoid, octodontiform, precordiform and variants within each of these types), as well as a relatively wide size range, comparable to that of the Santacrucian. This morphologic diversity shows that for the Colhuehuapian caviomorphs had already developed a large variety of adaptive types and strategies to use of food resources.

From an evolutionary point of view the Colhuehuapian rodent fauna is characterized by the richness of small octodontoids with a mosaic of “derived” and “primitive” characters, and by the great diversity of erethizontids that have their acme here. Hypsodont taxa are represented mainly by lineages different from those prevailing in younger faunas. Most Colhuehuapian rodents belong to lineages not recorded in post Middle Miocene faunas; only Eocardiids and Chinchillids, still little diversified, are certainly closely related to extant representatives.

Several questions concerning Colhuehuapian rodents are still poorly explored: 1) which factors promoted one of the highest peaks in diversity of fossil rodents in South America to be reached during the Colhuehuapian, and what particular conditions in Patagonia allowed the existence of such a wide diversity of octodontoids and erethizontids,

2) what selective pressures may have conditioned the disappearance of some lineages like cephalomyids, and the survival of others until today (chinchillids and caviids); palaeobiological studies are necessary to identify the ecomorphological features that would have favoured the selective survival of hypsodont taxa.

These and other questions will be answered as new data enlarge the knowledge of rodents from previous and subsequent faunas, and when more inclusive phylogenetic studies, especially of the enigmatic octodontoids are available.

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REFERENCES

Ameghino, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el museo de La Plata. *Bol. Museo de La Plata* **1**: 1–26.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas Acad. Nac. de Cs. en Córdoba* **6**: 1–1027.

Ameghino, F. 1897. Mammifères crétacés de l´Argentine. Deuxième contribution a la connaissance de la faune mammalogique des couches a *Pyrotherium. Bol. Inst. Geográfico Argentino* **18**: 406–29, 431–521.

Ameghino, F. 1898. *Sinopsis geológico - paleontológica de la Argentina*. Segundo Censo de la República Argentina **1**: 111–255.

Ameghino, F. 1899. *Sinopsis geológico-paleontológica*. Suplemento (Adiciones y correcciones). 13 pp. Imp. La Libertad, La Plata.

Ameghino, F. 1901. L'âge des formations sédimentaires de Patagonie. *Anales Soc. Cient. Argentina* **52**: 189-197; 244–50.

Ameghino, F. 1902. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. *Bol. Acad. Nac. de Ciencias en Córdoba* **17**: 71–138.

Ameghino, F. 1903. Los diprotodontes del orden de los Plagiaulacoideos y el origen de los roedores y de los polimastodontes. *Anales Mus. Nac Buenos Aires* **9** (3, 1): 81–192.

Ameghino, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales Soc. Cient. Argentina* **58**: 35-41, 56-71, 182-92, 225–91.

Barreda, V., and Palazzesi, L. 2007. Patagonian vegetation turnovers during the Paloegene-early Neogene: origin of arid adapted floras. *The Botanical Review* **73.**

Barreda, V., and Palazzesi, L. Vegetation during the Eocene – Miocene interval in central Patagonia: context of mammal evolution. *This book.*

Bellosi, E.S. Loessic and fluvial sedimentation of Sarmiento Formation pyroclastics in the middle Cenozoic of Central Patagonia. *This book.*

Bellosi, E.S., and González, M.G. Paleosols of the middle Cenozoic Sarmiento Formation, Central Patagonia. *This book*

Bordas, A.F. 1939. Diagnosis sobre algunos mamíferos de las capas con *Colpodon* del Valle del Río Chubut (República Argentina). *Physis* **14**: 413–33.

Candela, A.M. 1999. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *Parasteiromys* Ameghino, 1904. *Palaeovertebrata* **28**: 53–73.

Candela, A.M. 2000. *Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina. Sistemática e historia evolutiva evolutiva y biogeográfica*. PhD Dissertation, Universidad Nacional de La Plata, Argentina, 352 pp + 63 figs. Unpublished.

Candela, A.M. 2003. A new porcupine (Rodentia, Hystricognathi, Erethizontidae) from the Early - Middle Miocene of Patagonia. *Ameghiniana* **40**: 483–94.

Candela, A.M., and Morrone, J.J. 2003. Biogeografía de puercoespines neotropicales (Rodentia, Hystricognathi): Integrando datos fósiles y actuales a través de un enfoque panbiogeográfico. *Ameghiniana* **40**: 361–78.

Candela, A.M., and Vucetich, M.G. 2002. *Hypsosteiromys* (Rodentia, Hystricognathi) from the Early Miocene of Patagonia (Argentina), the only Erethizontidae with tendency to hypsodonty. *Geobios* **35**: 153–61.

Candela A.M. and Picasso M. In press. Inferring locomotor behavior in the Miocene porcupines (Rodentia, Erethizontidae). *J. Morph.*

Carvalho, G.A., and Salles, L.O. 2004. Relationships among extant and fossil echimyids (Rodentia, Hystricognathi). *Zool. J. Linn. Soc*. **142**: 445–77.

Croft, D., Flynn, J., and Wyss, A. 2004. Notoungulata and Litopterna of the Early Miocene Chucal Fauna, Northern Chile. *Fieldiana*: *Geology*, n. ser. **50**: 1–52.

Emmons, L.H., and Feer, F. 1990. *Neotropical Rainforest Mammals. A Field Guide*, 281 pp. The University of Chicago Press.

Emmons, L.H., and Vucetich, M.G. 1998. The identity of Winge's *Lasiuromys villosus* and the Description of a New Genus of Echimyid Rodent (Rodentia: Echimyidae). *Am. Mus. Nov*. **3223**: 1–12.

Flynn, J.J., Wyss, A.R., Charrier, R., and Swisher, C.C. 1995. An Early Miocene anthropoid skull from the Chilean Andes. *Nature* **373**: 603–7.

Frailey, C.D. 1980. *Studies on the Cenozoic vertebrata of Bolivia and Peru*. iii+ 257 pp. PhD Dissertation. Faculty of Graduate School University of Kansas, Lawrence.

Frailey, C.D., and Campbell, K.E. Jr. 2004. Paleogene rodents from Amazonian Peru: the Santa Rosa Local Fauna. In: *The Paleogene Mammalian Fauna of Santa Rosa,*

Amazonian Peru, ed. K. E. Campbell Jr., pp. 71–130. *Natural history Museum of Los Angeles County*, Science Series **40**: 1–163; Los Angeles.

Hershkovitz, P. 1958. A Geographic Classification of Neotropical Mammals. *Fieldiana Zoology* **36** (6): 581–620.

Hoffstetter, R., and Lavocat, R. 1970. Découverte dans la Déséadien de Bolivie de genres pentalophodontes appuyant les affinités africaines des Rongeurs Caviomorphes. *C. R. Acad. Sc. Paris* **271** (2): 172–175.

Kraglievich, J.L. 1965. Spéciation phylétique dans les rongeurs fossiles du genre *Eumysops* Amegh. (Echimyidae, Heteropsomyidae) *Mammalia* **29**: 258–267.

Kraglievich, L. 1926. Los grandes roedores terciarios de la Argentina y sus relaciones con ciertos géneros pleistocenos de las Antillas. *Anales Mus. Nac. Hist. Nat.* **34**: 121–135.

Kraglievich, L. 1930. La formación Friaseana del río Frías, río Fénix, Laguna Blanca, etc. y su fauna de mamíferos. *Physis* **10** (35): 127–161

Kraglievich, L. 1934. *La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que precedieron y sucedieron*, 136 pp., Imprenta "El Siglo Ilustrado", Montevideo.

Kraglievich, L. 1940. Descripción detallada de diversos roedores argentinos terciarios clasificados por el autor. *Obras de Geología y Paleontología* **1**: 297–330.

Kramarz, A.G. 1998. Un nuevo dasyproctidae (Rodentia, Caviomorpha) del Mioceno inferior de Patagonia. *Ameghiniana* **35**: 181–192.

Kramarz, A.G. 2001a. Registro de *Eoviscaccia* (Rodentia, Chinchillidae) en estratos colhuehuapenses de Patagonia, Argentina. *Ameghiniana* **38**: 237–242.

Kramarz, A.G. 2001b. Revision of the family Cephalomyidae (Rodentia, Caviomorpha) and new cephalomyids from the Early Miocene of Patagonia. *Palaeovertebrata* **30**: 51–88.

Kramarz, A.G. 2001c. *Prostichomys bowni*, un nuevo roedor Adelphomyinae (Hystricognathi, Echimyidae) del Mioceno medio - inferior de Patagonia, Argentina. *Ameghiniana* **38**: 163–168.

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

Kramarz, A.G. 2005 A primitive cephalomyid hystricognath rodent from the Early Miocene of northern Patagonia, Argentina. *Acta Paleont. Polonica* **50** (2): 249–258.

Kramarz, A.G. 2006. Eocardiids (Rodentia, Hystricognathi) from the Pinturas Formation, late Early Miocene of Patagonia, Argentina. Ms. de 26 pp., 6 figs. *J. Vert. Paleont*. **26** (3): 770–778

Landry, S.O. 1957. The interrelationships of the New and Old World Hystricomorph Rodents. *Univ. of California Publ. in Zool*. **56**: 1–118.

Loomis, F.B. 1914. *The Deseado Formation of Patagonia,* 232 pp., Rumford Press, Concord, Amherst.

Madden---- Bellosi this book.

Martin, T. 2005. Incisor Schmelzmuster diversity in South America's oldest rodent fauna and early caviomorph history. *J. mamm. Evol.* **12** (3-4): 405–417.

Pascual, R., Ortiz Jaureguizar, E., and Prado, J.L. 1996. Land mammals: Paradigm for Cenozoic South American Geobiotic Evolution. *Münchner Geowiss. Abh* (A) **30**: 265–319.

Patterson, B. 1958. A new genus of erethizontid rodents from the Colhuehuapian of Patagonia. *Beviora Mus. of Comp. Zool.* **92**: 1–4

Patterson, B., and Pascual, R. 1968. New echimyid rodents from the Oligocene of Patagonia and a Synopsis of the family. *Beviora Mus. Comp. Zool.* **401**: 1–14.

Patterson, B., and Wood, A.E. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bull. Mus. Comp. Zool.* **149**: 371–543.

Pérez, M.E., Kramarz, A., and Vucetich, M.G. 2005. Hallazgo del primer Eocardiidae (Rodentia) en el Mioceno inferior de la Formación Sarmiento aflorante en Bryn Gwyn (Gaiman, Chubut). *Ameghiniana* **42** (4 Suppl.): 39R.

Scott, W.B. 1905. Mammalia of the Santa Cruz Beds. Volume V, Paleontology. Part III, Glires. In *Reports of the Princeton University Expeditions to Patagonia*, 1896-1899, ed. W. B. Scott, pp. 384–490, Princeton University. E. Schweizerbart'sche Verlag (E. Nägele): Stuttgart.

Simpson, G.G. 1940. Review of the mammal-bearing Tertiary of South America. *Proc. Am. Philos. Soc.* **83** (5): 649–709.

Verzi, D.H. 2002. Patrones de evolución morfológica en Ctenomyinae (Rodentia, Octodontidae). *Mastozoología Neotropical* **9**: 309–328.

Vucetich, M.G. 1984. Los roedores de la Edad Friasense (Mioceno medio) de Patagonia. *Rev. Mus. La Plata* (Nueva Serie) 8 Paleontología **50**: 47–126.

Vucetich, M.G. 1985. *Cephalomyopsis hipselodontus* gen. et sp. nov. (Rodentia, Caviomorpha, Cephalomyidae) de la Edad Colhuehuapense (Oligoceno tardío) de Chubut, Argentina. *Ameghiniana* **22**: 243–245.

Vucetich, M.G. 1989. Rodents (Mammalia) of the Lacayani fauna revisited (Deseadan, Bolivia). Comparison with new Chinchillidae and Cephalomyidae from Argentina. *Bull. Mus. Nat. d´ Hist. Nat.*, Paris 4ª sér. 11, section C **4**: 233–247.

Vucetich, M.G., and Bond, M. 1984. Un nuevo Octodontoidea (Rodentia, Caviomorpha) del Oligoceno tardío de la provincia de Chubut (Argentina). *Ameghiniana* **21**: 105–114.

Vucetich, M.G., and Kramarz, A.G. 2003. New Miocene rodents of Patagonia (Argentina) and their bearing in the early radiation of the octodontiform octodontoids. *J. Vert. Paleont*. **23**: 435–444.

Vucetich, M.G., Mazzoni, M.M., and Pardiñas, U. F. J. 1993. Los roedores de la Formación Collón Cura (Mioceno Medio), y la Ignimbrita Pilcaniyeu. Cañadón del Tordillo, Neuquén. *Ameghiniana* **30**: 361–381.

Vucetich, M.G., and 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., and Verzi, D.H. 1993. Un nuevo Chinchillidae del Colhuehuapense (Mioceno Inferior?) de Gaiman (Chubut): su aporte a la comprensión de la dicotomía vizcachas - chinchillas. *Ameghiniana* **30**: 115.

Vucetich, M.G., and Verzi, D.H. 1994. The presence of *Protadelphomys* (Rodentia, Echimyidae) in the Colhuehuapian of South Barrancas of Lake Colhue Huapi (Chubut). *Ameghiniana* **31**: 93–94.

Vucetich, M.G., and Verzi, D.H. 1996. A peculiar octodontoid (Rodentia, Caviomorpha) with terraced molars from the lower Miocene of Patagonia (Argentina). *J. Vert. Paleont.* **16**: 297–302.

Vucetich, M.G., and Vieytes, E.C. 2006. A Middle Miocene primitive octodontoid rodent and its bearing on the early evolutionary history of the Octodontoidea. *Palaeontographica Abt.* A **27**: 79–89.

Vucetich, M.G., Verzi, D.H., and Dozo, M.T. 1992. El "status" sistemático de *Gaimanomys alwinea* (Rodentia, Caviomorpha, Echimyidae). *Ameghiniana* **29**: 85–86.

Walton, A.H. 1997. Rodents. In *Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*, eds. R.H. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn, pp. 392–409, Smithsonian Instit. Press, Washington.

Wood, A.E. 1949. A new oligocene rodent genus from Patagonia. *Am. Mus. Novitates* **1435**: 1–54

Wood, A.E., and Patterson, B. 1959. Rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bull. Mus. Comp. Zoo*l. **120**: 281–428.

Woods, C.A. 1984. Hystricognath rodents. In *Orders and families of recent mammals of the World*, eds. S. Anderson and J.K. Jones, pp. 384–446, John Wiley and Sons: New York.

FIGURE and TABLE CAPTIONS

Fig. 1: Location map**.**

Fig. 2: Dental diversity among Colhuehuapian rodents. **1,** *Eosteiromys homogenidens* MPEF 6097, right M1-2; **2,** *Hypsosteiromys axiculus* MACN A 52-171, right m1-3 (Holotype of *Steiromys axiculus*); **3,** *Galileomys antelucanus* MPEF 5418, right p4-m3 (reversed); **4,** *Prospaniomys priscus* MPEF 5627, left p4-m3; **5,** *Prospaniomys* sp.1 MPEF 7574a, right P4-M2; **6,** *Protacaremys prior* MPEF 5662, left dp4-m3; **7,** *Protacaremys avunculus* MACN A 52-126 right p4-m3 (holotype); **8,** *Protacaremys*? sp. nov. MEF 7557a, right m1-2; **9,** *Acarechimys* sp. MLP 82-V-2-40, right DP4; **10,** *Acarechimys pulchellus* comb. nov. MACN A 52-128 (Holotype of *P. pulchellus*), **a**, left p4-m3, **b,** left mandible in labial view; **11,** *Caviocricetus* MPEF 5419, right DP4-M2; **12,** Octodontoidea gen. et sp. nov. MPEF 5420, left m2-3; **13,** *Protadelphomys* morphotype A, MLP 82-V-2-30, left M1-2.

Fig. 3**.** Dental diversity among Colhuehuapian rodents (cont.). **1,** Dasyproctidae indet. MACN A 52-163, right upper molar, **a,** occlusal view, **b,** lingual view; **2,** *Luantus initialis* MPEF 6056, right P4-M2; **3,** *Perimys incavatus* MPEF 6755, right p4-m3; **4,** *Perimys dissimilis* MPEF 6754, right p4-m3; **5,** *Eoviscacia australis* MPEF 5422a, left p4 (inverted); **6,** *Eoviscacia australis* MPEF 5422b, left DP4; **7,** *Soriamys* sp. MPEF 6934c, right DP4?; **8,** Chinchilloidea incertae sedis MPEF 5421, upper molar.

Table 1. Colhuehuapian rodent record.