

# REVISION OF THE FAMILY CEPHALOMYIDAE (RODENTIA, CAVIOMORPHA) AND NEW CEPHALOMYIDS FROM THE EARLY MIOCENE OF PATAGONIA

by

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## CONTENTS

	Page
Abstract .....	52
Résumé .....	52
Resúmen .....	53
Introduction .....	54
Abbreviations .....	55
Systematic Paleontology .....	55
<i>Soriamys</i> gen. nov. ....	55
<i>Soriamys gaimanensis</i> sp. nov. ....	56
<i>Soriamys ganganensis</i> sp. nov. ....	67
Discussion .....	75
Conclusions .....	79
Acknowledgments .....	79
Tables 1-5 .....	80
Literature cited .....	86

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**Key-words:** Rodentia, Cephalomyidae, *Soriamys*, Lower Miocene, Patagonia, Systematics.

## ABSTRACT

A new genus of hystricognath rodent with two new species, *Soriamys gaimanensis* and *Soriamys ganganensis*, from the Colhuehuapian Age (Early Miocene), Sarmiento Formation, of Patagonia is described. The first species comes from the south barranca of the valley of Rio Chubut, near Gaiman locality (Chubut Province). It is known through a great number of dental remains in different stages of wear. The teeth are protohypsodont, with cement in the principal valleys. P4 are simpler, more oval in outline and without a differentiated hypocone-hypoflexus. Upper molars are pentalophodont in early stages of wear and become bilobated in middle and advanced stages; M3 have a temporary third posterior lobe due to the maintenance of the braquiflexus on the posterior wall of the tooth. Lower teeth have a completely asymmetrical pattern in relation to the uppers. The molars are trilophodont, with only one complex crest in the trigonid composed of the fusion of the anterolophid and mesolophid. The dp4 have a derived pentalophodont pattern due to the loss or fusion of the mesolophid and the development of an accessory transverse crest between the anterolophid and metalophid. The second species is known through a complete skull and jaw and other skull fragments with the dentition, proceeding from Pampa de Gan Gan, Chubut province. Respect to the first species, the teeth are higher crowned, with an earlier occlusal simplification and a third posterior lobe of M3 more developed and persistent. The skull and jaws show many chinchilloid characters, such as jugal bone with an ascending process, concave palate, very prominent dorsal shelf of the masseteric fossa, nasolachrymal duct opened laterally on the maxillary and very developed lateral mandibular fossa. Moreover, *Soriamys* is closely related to *Cephalomys* by sharing a similar asymmetric dental pattern and other dental and mandibular characters. These two genera constitute a natural group, the Cephalomyidae, with peculiar dental characters, like the asymmetric pattern of the upper and lower teeth; *Cephalomyopsis*, and probably *Litodontomys*, can be considered part of this group. *Scotamys* and *Perimys* constitute a distinct lineage (the Neopiblemidae or Perimyidae), more closely related to the chinchillids. Many characters shared by cephalomyids, eocardiids and caviids suggest a closer affinity between the Chinchilloidea and the Cavioiidea as a whole. *Abrocoma* shows also an asymmetric dental pattern and other chinchilloid features that suggest some degree of relationship with the cephalomyids, still not well determined.

## RESUME

On présente ici un nouveau genre de rongeur hystricognathe composé de deux nouvelles espèces, *Soriamys gaimanensis* et *Soriamys ganganensis*, du Colhuehuapien (Miocène inférieur) de la formation Sarmiento (Patagonie). La première espèce provient du ravin sud de la vallée du fleuve Chubut, à proximité de la localité de Gaiman (Province du Chubut). Elle comprend un grand nombre de restes dentaires à différents stades d'usure. Les dents sont protohypsodontes et possèdent du ciment dans les vallées principales. Les P4 sont simples, de forme ovale et sans différenciation hypocone-hypoflexus. A leur premier stade de croissance, les molaires supérieures sont pentalophodontes puis deviennent bilobées à des stades plus avancés ; les M3 ont provisoirement un troisième lobe postérieur due à la persistance du braquiflexus sur la paroi postérieure de la dent. Les dents inférieures sont complètement asymétriques par rapport aux dents supérieures. Les molaires sont trilophodontes avec une seule crête complexe sur le trigonide, fusion de l'antérolophide et du mésolophide. La dp4 a une forme dérivée pentalophodonte due à la perte ou à la fusion du mésolophide et au développement d'une crête accessoire transverse entre l'antérolophide et le métalophide. La seconde espèce, qui provient de la Pampa de Gan Gan, province du Chubut, est connue par un crâne et une mandibule complète ainsi que par plusieurs fragments crâniens portant des dents. Par rapport à la première espèce, les dents sont plus hypsodontes avec une simplification précoce de la surface occlusale et le troisième lobe postérieur de la M3 plus développé et persistant. Le crâne et les mandibules présentent plusieurs caractères chinchilloïdes comme le jugal possédant un processus ascendant, le palais concave, le bord dorsal de la fosse massétérique fortement

proéminent, le canal nasolacrymal ouvert latéralement sur le maxillaire et la fosse mandibulaire fortement développée latéralement. De plus, le partage de l'asymétrie dentaire ainsi que d'autres caractères dentaires et mandibulaires rapprochent *Soriamys* de *Cephalomys*. Ces deux genres constituent un groupe naturel, les Cephalomyidae, qui possèdent des caractères dentaires particuliers comme la forme asymétriques des dents supérieures et inférieures ; *Cephalomyopsis*, et probablement *Litodontomys*, peuvent être considérés comme appartenant à ce groupe. *Scotamys* et *Perimys* constituent une lignée distincte (les Neopiblemidae ou Perimyidae), plus fortement apparentée aux chinchillides. Plusieurs caractères partagés par les cephalomyidés, les eocardidés et les caviidés suggèrent une plus proche parenté entre les Chinchilloidea et les Cavioiidea. La présence chez *Abrocoma* d'un schéma dentaire asymétrique ainsi que d'autres caractères chinchilloides suggèrent que ce taxon montre un certain degré de parenté avec les cephalomyidés, ce qui n'est pas encore bien établi.

## RESUMEN

Se describe un nuevo género de roedor Hystricognathi con dos especies nuevas, *Soriamys gaimanensis* y *Soriamys ganganensis*, de la Edad Colhuehuapense (Mioceno temprano), Formación Sarmiento, de Patagonia. La primera especie proviene de la barranca sur del valle del Rio Chubut, próximo a la localidad de Gaiman. Es conocida por un gran número de restos dentarios en diferentes estados de desgaste. Los dientes son protohypsodontes, con cemento en los valles principales. El P4 es más simple, de contornos más ovalados y sin hipocono-hipoflexo diferenciado. Los molares superiores son pentafodotes en estadios juveniles y se tornan bilobulados en estadios medios y avanzados de desgaste; los M3 presentan un tercer lóbulo posterior temporario producto de la persistencia del braquiflexo sobre la pared posterior del diente. Los dientes inferiores presentan un patrón oclusal completamente asimétrico en relación a los superiores. Los molares son trifodotes, con sólo una cresta compleja en el trigónido compuesta por la fusión del anterolóbido y mesolóbido. El dp4 presenta un patrón pentafodonte derivado de la pérdida o fusión del mesolóbido y el desarrollo de una cresta transversal accesoria entre el anterolóbido y el metalóbido. La segunda especie es conocida por un cráneo y mandíbula completos y otros fragmentos craneanos con dentición, procedentes de Pampa de Gan Gan, provincia del Chubut. Con respecto a la primera especie, los dientes son de corona más alta, con una simplificación oclusal más temprana y tercer lóbulo posterior del M3 más desarrollado y persistente. El cráneo y mandíbula muestran varios caracteres propios de los chinchilloideos, como el yugal con proceso ascendente, paladar cóncavo, borde dorsal de la fosa maseterica muy prominente, ducto nasolacrimonal abierto lateralmente sobre el maxilar y fosa mandibular lateral muy desarrollada. Además, *Soriamys* está estrechamente relacionado a *Cephalomys* por compartir un patrón dentario asimétrico similar y otros caracteres dentarios y mandibulares. Estos dos géneros constituyen un grupo natural, los Cephalomyidae, con caracteres dentarios particulares, como la asimetría entre el patrón dentario superior y el inferior; *Cephalomyopsis*, y probablemente *Litodontomys*, pueden ser considerados parte de este grupo. *Scotamys* y *Perimys* constituyen un linaje distinto (los Neopiblemidae o Perimyidae), más cercanamente relacionados a los chinchillidos. Varios caracteres compartidos por los cefalómidos, eocardidos y cávidos sugieren una mayor afinidad entre los Chinchilloidea y los Cavioiidea en su conjunto. *Abrocoma* presenta también un patrón dentario asimétrico y otros rasgos de chinchilloideo que sugieren algún grado de parentesco con los cefalómidos, aún no bien establecido.

## INTRODUCTION

The initial period of the hystricomorph rodents evolution in South America shows that several groups with a strong tendency for hypsodonty differentiated very early (chinchilloids, cavioids and to a lesser extent dasyproctids), while others, like octodontoids, developed such attribute much later (Vucetich, 1986). The three first mentioned lineage are already present in the Deseadan and each one already exhibits particular dental features: *Eoviscaccia* VUCETICH, 1989 has transversal compressed laminae, like in later chinchillids; *Asteromys* AMEGHINO 1897 and *Chubutomys* WOOD & PATTERSON, 1959 already show molars formed by two triangular lobes with acute extremities, like in the more advanced eocardiids and caviids; *Incamys* HOFFSTETTER & LAVOCAT, 1970 has an advanced development of an occlusal scheme "S" shaped.

The existence of another group, the "Cephalomyidae" AMEGHINO, 1897, formed by *Cephalomys* AMEGHINO, 1897 and other early hypsodont genera (*Scotamys* LOOMIS, 1914; *Litodontomys* LOOMIS, 1914; *Perimys* AMEGHINO, 1887 and *Cephalomyopsis* VUCETICH, 1985), was recognized by Loomis (1914), Miller and Gidley (1918) and Landry (1957), and revalidated by Vucetich (1985). The relationships of these genera among themselves and with other caviomorphs vary depending on the authors (see Wood and Patterson, 1959; Vucetich, 1985; McKenna and Bell, 1998) and even the validity of the family is still controversial.

The taxonomic fluctuations of *Cephalomys* and its relatives seem to be the result of the lacking of a more accurate dental characterization rather than the mere fact to be hypsodont. Moreover, its occlusal morphology is strongly simplified, hiding the homologies of crown structures. Such simplification would have produced in *Cephalomys* a occlusal configuration similar to the ancestors of other hypsodont groups, but not necessarily homologous. The scarce cranial remains available of *Cephalomys* are very fragmentary and do not show diagnostic features enough to classify it in an unmistakable way into one or other group; except for *Cephalomys* and *Perimys*, "cephalomyids" are known only by their teeth.

In this paper, a new genus allied to *Cephalomys*, represented by two species coming from exposures of the Sarmiento Formation is presented. One species is known through numerous isolated teeth, in different stages of wear, from the south barranca of the Rio Chubut, in front of Gaiman locality, Chubut province, Argentina; the other is known through a complete skull and jaw and other cranial remains with the dentition, from the Pampa de Gan Gan, 250 km. northwest from the first one (see figure 1). Both localities are assigned to the Colhuehuapian Age (Simpson, 1935, Mendia and Bayarsky, 1981).

The study of these remains enlarges the knowledge on the dental morphology transformations related to the development of the hypsodonty in the earliest caviomorphs. It also allows the evaluation of the validity and extension of the family Cephalomyidae and its relationships to other caviomorphs groups.

The studied materials were collected during the expeditions made jointly by the Museo Argentino de Ciencias Naturales and the State University of New York, directed by J. G. Fleagle and M. F. Soria.

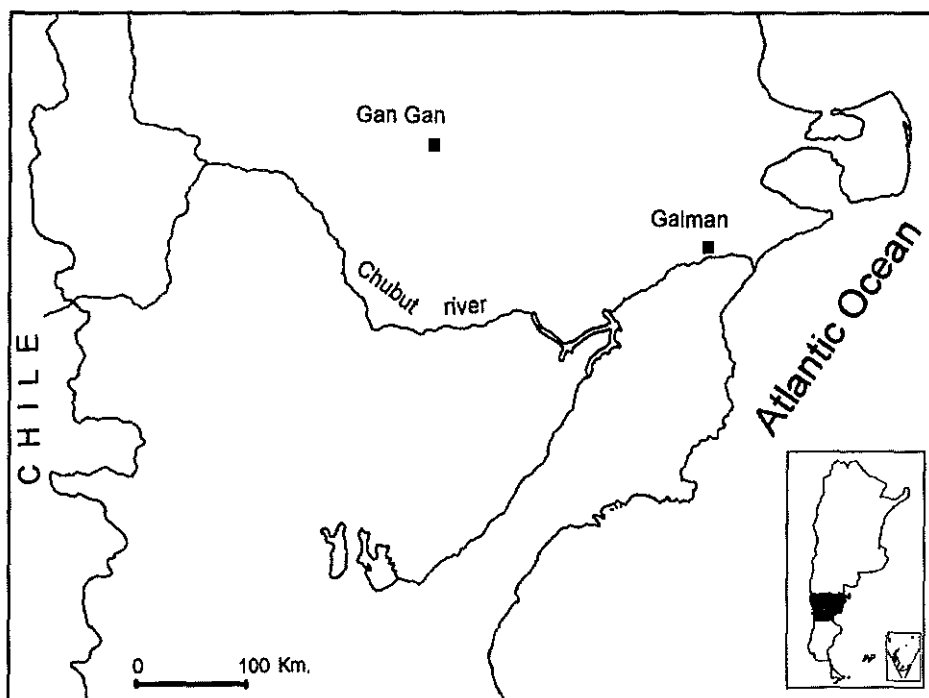


Figure 1.— Map of Chubut province, Argentina, showing the location of the fossil localities.

## ABBREVIATIONS

MACN - Museo Argentino de Ciencias Naturales "Bernardino Rivadavia".

MLP - Museo de La Plata

CNP - Centro Nacional Patagónico

## SYSTEMATIC PALEONTOLOGY

Order **RODENTIA** BOWDICH, 1821

Suborder **HYSTRICOGNATHI** TULLBERG, 1899

Infraorder **CAVIOMORPHA** WOOD & PATTERSON *in* Wood, 1955

Family **CEPHALOMYIDAE** AMEGHINO, 1897

*SORIAMYS* gen. nov.

**Type species:** *Soriamys gaimanensis* sp. nov.

**Etymology:** In honor and acknowledgment to Miguel F. Soria and for his labor in the

M.A.C.N.

**Chronologic and geographic distribution:** Colhuehuapian Age (Early Miocene, Flynn and Swisher, 1995); Chubut Province, Argentina.

**Diagnosis:** Caviomorph with very high crowned teeth. Flexa and flexids with cement. P4 without a differentiated hypoflexus - hypocone, as in *Cephalomys*, *Luantus*, *Eocardia* and *Perimys*; bilophodont, paracone more closely related to anteroloph than in *Platypittamys* and *Deseadomys*. M1-2 bilobated by the deep transverse penetration of the hypoflexus. M3 trilobated, with the third lobe formed essentially by the metaloph. Protocone anterior to paracone and hypocone anterior to metacone. Lower permanent teeth trilophodont in every stages of wear due to the early fusion of the two anterior crests. Hypoflexid opens posterolabially. Protoconid posterior to metaconid and hypoconid posterior to entoconid.

*Soriamys gaimanensis* sp. nov.

(Figures 3 to 7)

**Holotype:** MACN CH 1800, a fragment of left maxilla with P4 and M1.

**Hypodigm:** The holotype and the following specimens: MACN CH 197, left isolated m1or 2; MACN CH 1801, left isolated P4; MACN CH 1802, right isolated P4; MACN CH 1803, right isolated P4; MACN CH 1804, right isolated P4; MACN CH 1805, left M1or 2; MACN CH 1806, left M1or 2; MACN CH 1807, right M1or 2; MACN CH 1808, left M1or 2; MACN CH 1809, left M1or 2; MACN CH 1810, left M1or 2; MACN CH 1811, right M3; MACN CH 1812, left M3; MACN CH 1813, left M3; MACN CH 1814, left M3; MACN CH 1815, left M3; MACN CH 1816, left M3; MACN CH 1817, left M3; MACN CH 1818, right M3; MACN CH 1819, right M3; MACN CH 1820, left M3; MACN CH 1821, left M1or 2; MACN CH 1822, right M1or 2; MACN CH 1823, left M1or 2; MACN CH 1824, right M1or 2; MACN CH 1825, left M1or 2; MACN CH 1826, right M1or 2; MACN CH 1827, left dp4; MACN CH 1828, right jaw fragment with m2 and m3; MACN CH 1829, right jaw fragment with the m1 and the roots of the premolar; MACN CH 1830, left isolated m1?; MACN CH 1831, left m1or 2; MACN CH 1832, right M1or 2 ; MACN CH 1833, right DP4; MACN CH 1834, right dp4; MACN CH 1835, left DP4; MACN CH 1836, right p4; MACN CH 1837, right p4; MACN CH 1838, six isolated upper molars; MACN CH 1839, left M3; MACN CH 1840, right m1or 2; MACN CH 1841, left M1or 2; MACN CH 1842, nine isolated upper molars; MACN CH 1843, nine isolated upper molars; MACN CH 1844, eleven isolated upper molars; MACN CH 1845, eleven isolated upper molars; MACN CH 1846, fifteen isolated lower premolars; MACN CH 1847, sixty-one isolated lower molars; MACN CH 1848, two dp4 and six isolated lower molars; MACN CH 1849, four isolated upper and two lower molars; MACN CH 1850, a left isolated m1or 2.

**Etymology:** From Gaiman, Chubut Province, locality next to the site where all the specimens were found.

**Geographic provenance:** La Cantera (Bown and Fleagle, 1993), on the south barranca of Rio Chubut, next to Gaiman, Chubut Province, Argentina (figure 1).

**Stratigraphic provenance and age:** Lower part of Trelew Member, Sarmiento Formation (Simpson, 1935; Andreis et al., 1975; Mendia and Bayarsky, 1981; Fleagle and Bown, 1983; Bown and Fleagle, 1990), Colhuehuapian Age (Early Miocene) (Flynn and Swisher, 1995).

**Diagnosis.** Protohypsodont teeth, with the enamel layer discontinuous only on the base; cement is scant. Upper cheek teeth with fossettes persisting until middle stages of wear. M3 trilobated only during first stages of wear.

### **Description**

The teeth of *Soriamys gaimanensis* are high-crowned, with their growth limited by the late formation of the roots (protohypsodont). Most of the available M3 and m3 are larger than the remaining molars; all the P4 and p4 are smaller than the molars; a gradual backward increase in teeth size is deduced.

Cement is present filling the main valleys (hypoflexa and hypoflexids), and variable in the others; it does not reach the crown apex. The cement covers the vertical walls of the valleys: it is thinner at the external side, forming a deep vertical groove without cement.

The enamel layer is homogenous at the top of the crowns, but toward the base it is reduced or absent on the labial and posterior margins of the upper teeth (figures 4 D, E and F) and on the anterior and posterior borders of the lowers (see figures 6 C and D). These discontinuities seem to be the result of a reduction of enamel deposition rather than interdentary wear.

The jugal teeth show an evolutionary stage in which the cusps can not be differentiated because they are completely integrated to the loph and lophids. However, their locations can be inferred by the presence of small protuberances on the surface of the crests of unworn teeth, by the existence of thickenings of the crests, especially on their extremities, and by comparison with other hystricomorph rodents with cuspidate teeth (see figure 2).

Upper dentition. The premolars are subcylindrical, implanted with their base curving forward. They are composed basically by two laminae that converge lingually (see figure 3). In the only available unworn P4 (MACN CH 1801, see figure 3 A) there is a thickening on the lingual portion of the anterior lamina, that may correspond to the apex of the protocone. This lamina describes a gentle curve with a backward concavity and does not reach the lingual border of the tooth. The posterior lamina is transversal, scanty concave forward and forms the posterior border of the tooth. There is a thickening toward the labial end that may be displaying the metacone location. Assuming that the anterior lamina may involve to the protocone and the posterior to the metacone, they may be homologous to the anterior and posterior crests of *Gaudeamus* (WOOD, 1968) (see figure 2C), *Sallamys* (HOFFSTETTER & LAVOCAT, 1970) or *Platypittamys* (WOOD, 1949).

The anterior crest has a short labial derivation extending to the buccal margin, that may correspond to the paracone. The anterior crest and its derivation delimit a shallow vertical anterolabial groove (see figures 3 A and B) that does not extend up to the base of the tooth. This groove, that separates temporarily the anteroloph and the paracone, may be assumed to be homologous to the paraflexus of the premolars of other

hystricomorphs. In the type specimen (figure 3 D) there is not any trace of this groove, due to the more advanced wear, and the paracone joins directly the labial end of the anteroloph.

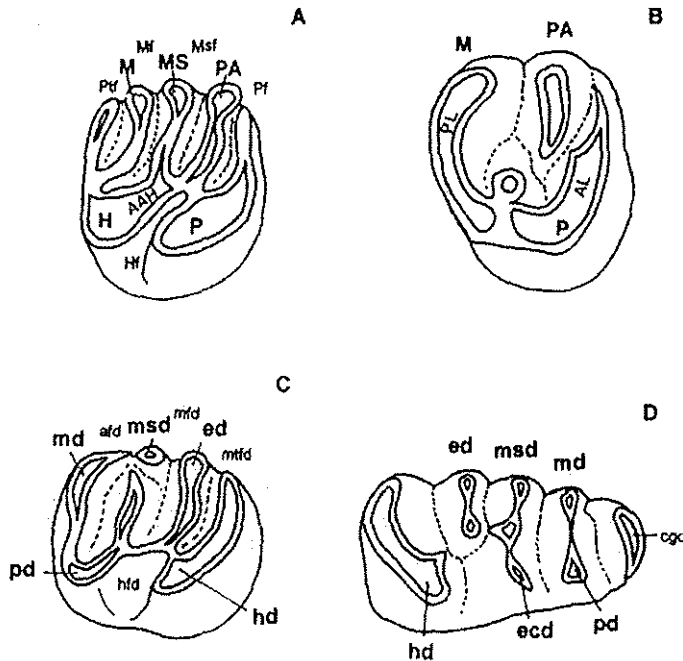


Figure 2.— Key to terminology applied to cusps, crests and valleys of the molariphorms. A: right upper molar of *Steiromys* sp. B: right upper premolar of *Gaudeamus aegyptus*. Abbreviations: AAH, anterior arm of hypocone; AL, anteroloph; H, hypocone; Hf, hypoflexus; M, metacone; Mf, metaflexus or metafossette; MS, mesostyle; Msf, mesoflexus or mesofossette; P, protocone; PA, paracone; Pf, paraflexus or parafossette; PL, posteroloph; Ptf, posterofossette. Transversal crests of upper molars, from anterior to posterior: anteroloph, mesoloph, metaloph and posteroloph. C: left lower molar of *Steiromys* sp. D: right lower deciduous premolar of *Gaudeamus aegyptus*. Abbreviations: afd, anteroflexid or anterofossettoid; cgd, anterior cingulum; ecd, ectostylid; ed, entoconid; hd, hypoconid; hfd, hypoflexid; md, metaconid; mfd, mesoflexid or mesofossettoid; msd, mesostylid; mtfd, metaflexid or metafossettoid; pd, protoconid. Transversal crests of lower molars, from anterior to posterior: anterolophid, mesolophid, hypolophid and posterolophid.

In the center of the premolar a deep valley separates the posteroloph and anteroloph. It opens labially during the first stages of wear, isolating the paracone and metacone (see figure 3 C). In more worn specimens the central valley is labially closed and adopts a subtriangular outline (figures 3 B and D).

The occlusal morphology of upper premolars of *S. gaimanensis* seems to be the result of the retention of the primitive tricuspidate pattern, over which would have operated an early process of occlusal simplification, as in *Perimys* and *Cephalomys*. The premolars of *Soriamys* resemble superficially those genera because they display a "reversed" occlusal pattern respect to the molars, i.e. with two laminae diverging and separated, at least temporary, at the labial side. However, in unworn or slightly worn premolars of *Perimys* (figure 8 B) and *Cephalomys* (see Wood and Patterson, 1959; figures 13 A and 14 A) three well developed crests are observed. The paraflexus is very



penetrating and remains labially open up to the base of the tooth, forming the main flexus; the second flexus is shallow and, with more wear, the crest of the paracone fuses with the posterior crest and the bilobated pattern is acquired. Contrarily, in *Soriamys* the paracone would be closely related to the anterior crest, resembling superficially the premolars of some primitive octodontoids, like *Deseadomys* and *Platypittamys*.

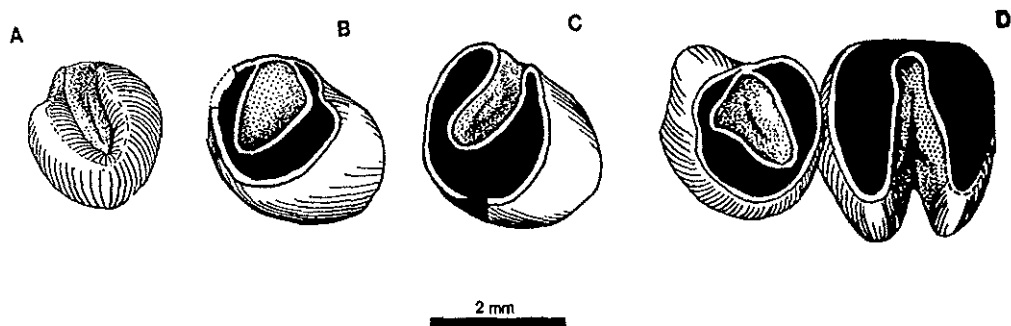


Figure 3.— *Soriamys gaimanensis* gen. et sp. nov. A: MACN CH 1801, unworn left upper premolar. B: MACN CH 1802, right upper premolar. C: MACN CH 1803, idem. D: MACN CH 1800 (holotype), fragment of left maxilla with P4 and M1.

Several isolated upper molars in different stages of wear have been recovered, consequently the successive changes of the occlusal morphology produced by wear may be analyzed. As usually, the differentiation between M1 and M2 is difficult when studying isolated teeth. The M3 is recognized through the characteristic development of its posterior region and its posterobuccal root.

Four arbitrary stages of wear for the M1 and M2 have been differentiated to make easier the description.

1) In a young state (see figure 4 A) a pentalophodont pattern can be observed.

- The anteroloph is nearly transverse and straight, it forms the whole anterior margin of the tooth. Its lingual extremity, the inferred location of the protocone, is gently acute.

- The protoloph is completely transverse; it is longer than half the transverse diameter of the tooth. The lingual extremity joints anteriorly with the anteroloph and posteriorly with the hypocone through the mure.

- The mesoloph extends transversally from the hypocone up to the labial margin, where it describes a slight curve backward, continuing then with the labial end of metaloph. The hypocone is very bulky, it is located more labially than the protocone and its anterior ramus is almost indistinguishable from the mure.

- The labial portion of the metaloph is thick, showing the location of the metacone. The lingual portion curves backward, reaching the posterior border where it converges with the posteroloph.

- The posteroloph is slightly lower than the other crests. It extends from the metacone to the hypocone, forming the posterobuccal margin of the tooth.

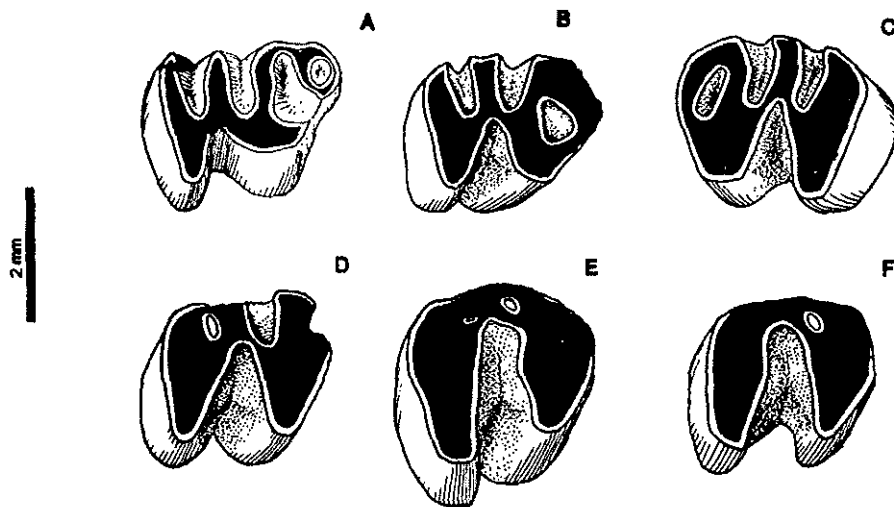


Figure 4.— *Soriamys gaimanensis* gen. et sp. nov. Upper molars A: MACN CH 1805, left M1 or 2. B: MACN CH 1806, left M1 or 2. C: MACN CH 1807, right M1 or 2. D: MACN CH 1808, left M1 or 2. E: MACN CH 1809, left M1 or 2. F: MACN CH 1810, left M1 or 2.

If the inferred locations of cusps are correct, then their relative positions turns out very peculiar: the protocone is situated more anteriorly than the paracone and, in an analogous way, the hypocone is anterior to the metacone.

The labial flexi are wide and lengthened. The metaflexus is the largest and rapidly becomes a fossette, usually "pear-like" in outline. The metaloph and the posteroloph delimit a small subcircular posterofossette confined to the posterobuccal angle. The hypoflexus is front of the paraflexus; it penetrates obliquely and is very wide. At this stage of wear the tooth is longer than wide, with the transverse diameter decreasing gradually back.

2) In a subsequent stage of wear (see figure 4 B and C) the crests become thicker and the flexi narrower. The hypoflexus extends transversally more than half way across the crown, opposite to the protoloph, not to the paraflexus, and nearly triangular in outline. The protoloph is reduced. The anterior ramus of the hypocone is conspicuous, thick and transversally elongated. The small posterofossette has disappeared due to the fusion of metaloph and posteroloph, which form a large surface at the posterolabial angle. The metafossette is remarkably reduced, and now it is smaller than the paraflexus and mesoflexus.

3) As wear continues (see figure 4 D) the hypoflexus penetration becomes more pronounced, with detriment to the extension of the protoloph. Then, an insinuation of a bilobated pattern begins. The anterior lobe is subtriangular in outline and is formed mainly by the protocone and the anteroloph. The posterior lobe is composed principally by the hypocone; it is usually transversally shorter and slightly broader than the former. Its lingual extremity is blunt in some specimens and rounded in others. At this stage the metaflexus disappears; the paraflexus, and little later the mesoflexus, become in subcircular fossettes located in the labial portion of the tooth. There is a reduction of the

posterior surface, so the anteroposterior diameter is almost equal to the transversal one. The wear effects are more pronounced on the posterior and labial borders.

4) In a very advanced stage of wear (see figure 4 E and F) the bilobated pattern is consolidated. The first lobe has its anterior margin a little more curved than the posterior margin. The second lobe is usually slightly shorter; its outline is similar to the first lobe but reversed, i.e. with the anterior margin straight and the posterior curved. The hypoflexus reaches the maximum penetration producing the maximum shortening of the protoloph, which constitutes the isthmus that joints both lobes. The faces of the hypoflexus are almost parallel, so the hypoflexus adopts a fork-like contour. The parafofsette and the mesofossette are very reduced or absent; the metafofsette may persist till terminal stages of wear.

These kind of changes in the occlusal morphology during the wear process are common in some protohypsodonts rodents, like *Eoviscaccia*, *Cephalomys* or *Luantus*. These changes use to follow some generalized patterns, like the reduction of the anteroposterior diameter, the hypoflexus deepening, the transformation of the labial flexi into small rounded fossettes limited in the buccal portion of the tooth, and the reduction of the number of crests (Schmidt-Kittler, 1984). Such transformations originate a lobular or laminar dental pattern. This pattern is acquired in *Soriamys* (and also in *Cephalomys* and *Luantus*) by the deep transversal penetration of the hypoflexus over the area initially occupied by the protoloph (see figure 6 C and F). On the contrary, in *Eoviscaccia* and *Scotamys* the hypoflexus penetrates diagonally over the paraflexus, so the enamel isthmus that separates both valleys is displaced labially; the protoloph loses its contact with the protocone, continuing with the mure and this one with the anterior ramus of the hypocone, forming a single structure that extends diagonally from the paracone to the hypocone, and suggesting temporarily a sigmoid pattern (see Vucetich 1989, plate I, figure b).

*Perimys* presents in very juvenile stages (see figure 8 A) a dental morphology very similar to that of *Soriamys* in middle stages of wear (compare with figure 4 C). However, The paraflexus and mesoflexus of the molars of *Perimys* never become fossettes, but they stay labially opened until they disappear in adult stages. The paraflexus usually remains like a vertical furrow on the external wall of the tooth, and its persistence is variable depending on the species. With the wear, the molar surface of *Perimys* modifies quickly into a two transverse laminae pattern separated by a thick deposit of cement, which is the same seen in terminal stages of *Soriamys*.

The M3s tend to adopt a laminar configuration at earlier stages than the M1s and the M2s, due to the deep transversal penetration of the hypoflexus with detriment to the length of the protoloph. The first lobe is rectangular, with the lingual end slightly rounded. The second lobe presents a similar geometry, but it is a little shorter in transverse direction, as in the M1 and M2. In the M3 the metaloph is much longer and thicker than in the other molars, and has a transverse orientation, not curved, parallel to the other crests. The posteroloph is reduced, appearing like a small rim on the posterior face of the metaloph, not on the occlusal surface; the posterofossette is represented by a simple horizontal notch in that position (see figure 5 B). During the first stages of wear, the lingual ends of the metaloph and of the posteroloph are largely separated from the hypocone, as the metaflexus remains open on the lingual margin, forming a

"braquiflexus" (Walton, 1990). Due to its greater development, the metaloph constitutes a real third lobe, parallel and shorter than the anterior lobes (see figures 5 A and B).

With wear (figure 5 C, D and E), the posteroloph of the M3 emerges on the occlusal surface and its lingual end contacts the hypocone, closing the braquiflexus and joining the extremities of the second and third lobes, which form a single one with triangular contour and slightly acute end. The anterior lobe does not show any important modifications with wear.

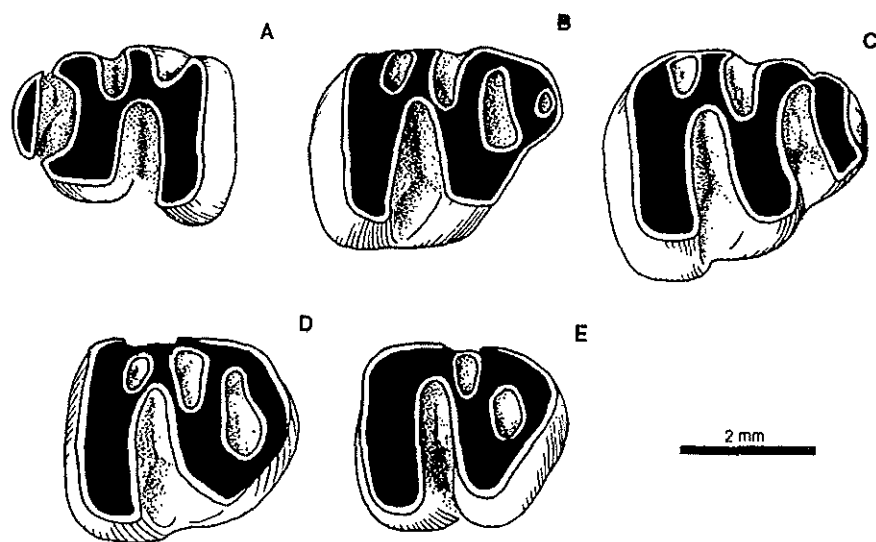


Figure 5.— *Soriamys gaimanensis* gen. et sp. nov. Upper M3s. A: MACN CH 1811, right M3. B: MACN CH 1812, left M3. C: MACN CH 1813, left M3. D: MACN CH 1814, left M3. E: MACN CH 1815, left M3.

The metaflexus is the largest of external flexi and, unlike the M1 and M2, its size is constant until a very advanced stage of wear. The parafofsette is the smallest and ephemeral. (see figures 5 D and E).

It is usual among the high crowned caviomorphs that the M3s have some specialization, developing a third lobe or lamina, as in chinchillids, caviids, eocardiids, hydrochoerids, *Scotamys*, *Perimys* and *Abrocoma*, but not in octodontids and capromyids. The nature of this third lobe in the M3 of cavioids can be well explained in *Luantus* (see figure 9 A): the posteroloph forms a posterior projection on the posterolabial border of the tooth, originating an accessory posterior flexus, different from the metaflexus, from which it is separated. The later development of this posterior extension of the M3 would give origin to the characteristic trilobated pattern of the more advanced eocardiids and caviids.

In *Soriamys* the trilobated pattern of the M3 is the result of a greater development of the metaloph and the persistence of the braquiflexus isolating the hypocone, at least temporarily. Until then, the aspect of the occlusal surface resembles that of the M3 of *Perimys*. *Eoviscaccia* does not show any sign of a third lobe, but it is already present in the M3 of *Prolagostomus*, with the same scheme of *Soriamys*. Probably this is the

mechanism that originated the typical third lamina in the modern chinchillids.

It is difficult to determine the homologies of the crests in *Abrocoma*. However the longitudinal disposition of the third lobe of M3, instead of transverse, may indicate that it was originated by a different mechanism from that of *Soriamys*.

The Dp4 referable to this species are mesodont, with well developed roots and the anteroposterior diameter notably larger than the transverse one. The occlusal surface has a very similar morphology to the molars in young stages of wear, although in one specimen (MACN CH 1835) the metafossette is divided in one small lingual fossette and other larger on the labial side.

Lower dentition. At first sight, lower and upper teeth do not match morphologically, and no associated upper and lower teeth have been registered. These lower teeth were assigned to *S. gaimanensis* first because they have the same size as the uppers, the same hypsodonty degree and the same relative abundance (85 upper and 88 lower cheek teeth have been recovered). Other morphological details described below confirm such assignation.

Almost all lower teeth have a clear trilophodont pattern (see figures 6 and 7). The p4 distinguishes in having only two roots (anterior and posterior); it is the smallest and its trigonid is narrower than its talonid (figure 7 C and D). The molars do not show significant morphological differences in the occlusal surfaces: consequently, their location in the dental row can only be inferred by the curvature of the vertical axis: the vertical axis of the m1 (figure 6 B) is almost straight and the anteroposterior diameter reduces toward the base, more than in the m2. The m3 are strongly curved and, on the contrary, the diameter increases toward the base. All the teeth recognized as m1 are slightly larger than the p4s and smaller than the m2 and m3.

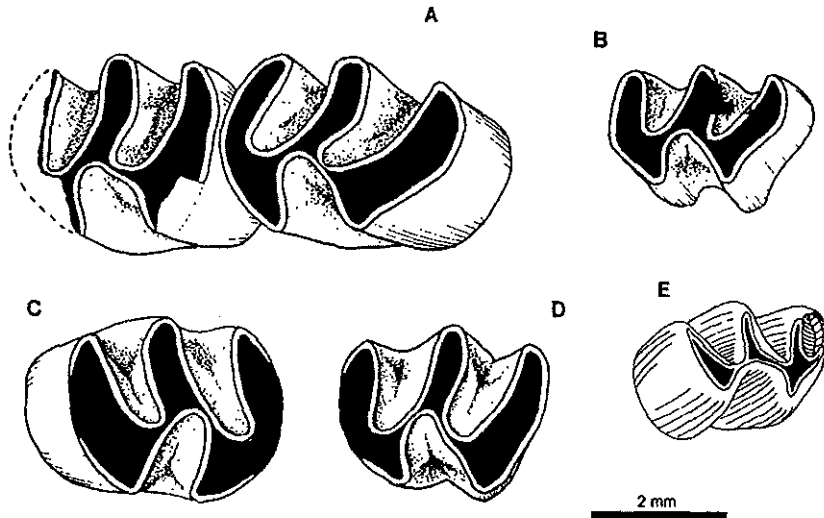


Figure 6.— *Soriamys gaimanensis* gen. et sp. nov. Lower molars. A: MACN CH 1828, left m2 and m3. B: MACN CH 1829, left m1. C: MACN CH 1831, right m2. D: MACN CH 1832, left m2?. E: MACN CH 1830, right m1.

It can be interpreted undoubtedly that the two last crests in all the lower teeth are the hypolophid and posterolophid. However, the nature of the anterior crest is dubious. Only one specimen (see figure 6 E) is little worn enough to observe that the trigonid is originally formed by two crests, the posterior is larger and constitutes the main part of the trigonid surface. These two structures may be homologous to the two anterior crests of the lower tetralophodont caviomorphs teeth, i.e. the anterolophid and the mesolophid. This interpretation is only tentative because even in this stage of wear neither a mesoconid nor a mesostylid is distinguished. Both crests are separated by a very ephemeral fossettid (anterofossettid), and the crests fuse rapidly with wear originating a single anterior crest. Because of the small size and the equal extension of the talonid and trigonid, this tooth would be a m1. This fossettid is not distinguished in any m2 or m3 in similar stage of wear, probably because the anterolophid and mesolophid are completely fused.

In the molars (see figure 6) the anterior composed crest forms the whole anterior border of the tooth and part of the labial border, it is strongly curved with the concavity backward. Its buccal end, where the protoconid would be located, is posteroexternally directed and is slightly acute. The lingual end, which is the inferred position of the metaconid, is rounded. In the p4 (figure 7 C and D) the anterior crest is straight and its labial end is directed labially.

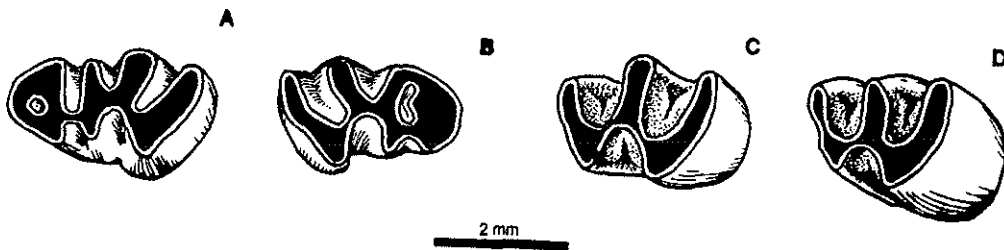


Figure 7.— *Soriamys gaimanensis* gen. et sp nov. Lower premolars. A: MACN CH 1834, left dp4. B: MACN CH 1827, right dp4. C: MACN CH 1836, left p4. D: MACN CH 1837, left p4.

The hypolophid starts nearly at the center of the crown and usually extends more lingually than the other crests. In the molars it is directed obliquely backward, and gradually becomes transverse at the lingual end. In the p4 the hypolophid is transverse and mainly straight. The ectolophid is very short, it is indistinguishable from the posterior branch of the protoconid and is obliquely disposed, joining the protoconid with the labial end of the hypolophid. The posterolophid is almost parallel to the hypolophid and to the lingual half of the anterior crest. Its buccal end, which is the inferred position of the hypoconid, is acute. The hypoconid is connected with the labial end of the hypolophid through a slender anterior ramus, arranged nearly parallel to the labial half of the anterior crest and perpendicular to the other crests.

The valleys are large and extend half way across crowns. The two lingual flexids are similar in size and outline, and remain open in all stages due to the absence of longitudinal crests joining the lingual ends of the lophids (see figure 6 C and D). The hypoflexid is triangular and penetrates obliquely forward; this character is more

conspicuous in the m2 and m3 (figure 6 A and C) and minimum in the p4 (see figure 7 C and D).

The occlusal surface presents the labial crests perpendicular to the lingual ones and both are oblique in relation to the anteroposterior axis. This pattern would be associated to the peculiar relative disposition of cusps: again, if the inferred locations of cusps are right, then the metaconid and the entoconid would be anterior to the protoconid and hypoconid respectively, which is analogous to what is observed in the upper molars. This "displacement" of cusps confirms the correct association of the upper and lowers molars.

According to the present interpretation, the trilophodonty of *Soriamys* is the result of the fusion of anterolophid and mesolophid (not the usual reduction of the latter), which resembles what happens in the m1 and m2 of *Cephalomys*. However, in this genus the metafossetid is also ephemeral, only persisting the mesofossetid, giving the characteristic octodontiform pattern, what is undoubtedly different from *Soriamys*. Neither *Perimys* and *Scotamys* nor any known chinchillid have an occlusal configuration similar to *Soriamys*. However, this pattern is suggestively similar to such unrelated genera like *Abrocoma*, *Echimys*, *Maruchito*, *Capromys* and *Chaetomys*. In all these cases this peculiar occlusal pattern is also associated with a strongly transverse crest disposition in the upper molars. Consequently, this character does not seem to be a good indicator of phylogenetical relationships, but it would be an answer to similar mechanic requirements, probably related to the parallel disposition of the tooth rows. It may be inferred that in *S. gaimanensis* the tooth rows were also disposed in that way.

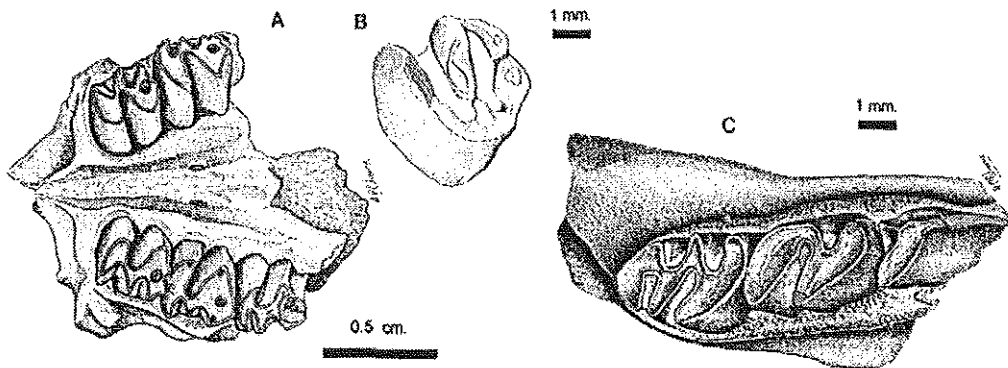


Figure 8.— *Perimys* sp. A: MLP 68-I-17-80, palate with partial dentition of a juvenile specimen. B: MLP 68-I-17-12, left unworn P4. C: MLP 15-80, left mandibular fragment of a juvenile specimen with dp4, m1 and the anterior portion of m2.

The dp4 of *S. gaimanensis* is easily distinguishable because it is mesodont, and its anteroposterior diameter is much longer than the transverse (see figure 7 A and B) caused by the characteristic anterior development of the trigonid. The occlusal pattern has five transversal crests, that seems to be the same pentalophodont pattern, considered ancestral (Hoffstetter and Lavocat, 1976), present in *Gaudeamus* (see figure 1 D). Comparing with the latter, it may be interpreted that in *Soriamys gaimanensis* the whole anterior margin of the dp4 is formed by the anterior cingulum, very developed,

that describes a semi-circumference. The following crest would be the metalophid, that extends transversally, connecting the extremities of the anterior crest; a small circular fossettid is delimited between the two first crest (figure 7 A) that disappear in more advanced stages of wear (figure 7 B). The two posterior crests, the hypolophid and the posterolophid, have the same size and disposition than those of the molars. The central crest would be the mesolophid and, unlike the molars, it is conspicuous. The mesolophid is separated from the metalophid by two opposed flexids, the labial one penetrates much deeper in the crown than the lingual one. It is separate from the hypolophid by two other opposed flexids with similar size and geometry; both flexids are separated from by a short longitudinal wall that may represent the ectolophid. If so, the mesolophid would have a derivation, labial to the ectolophid, that is unusual in caviomorphs, but which is present in *Gaudeamus* (figure 1 D). Such a labial derivation of the mesolophid suggests the persistence of an ectostylid, as in *Steiromys* and in some ctenodactiloids, as *Fallomus* or *Baluchimys* (Flynn *et al.* 1986).

According to this interpretation, the dp4 of *Soriamys* presents a very primitive pattern that contrasts with the derived character of its molars. There is another possible interpretation based upon the observation of the dp4 of other hypsodont genera. Although it is uncertain whether the crown structures of the premolars can be homologous to those occupying similar topographic locations in the molars, it may be interpreted that evolutionary changes of some elements of the molars, in this case the mesolophid, can be reflected in its correspondent serial homologous of the dp4. In this way, in *Luantus* (see figure 9 B), the mesolophid shows a slight reduction, both in molars and dp4; in *Neoreomys* and *Scleromys* the mesolophid is incomplete in all the lower teeth; in *Stichomys* and *Adelphomys* the mesolophid is notably reduced in molars as well as in premolars. In the case of *Soriamys*, the association of the mesolophid with an anterior crest in the molars can be extrapolated to the dp4, where it would be associated with the metalophid. If so, the central crest of the dp4 would be the result of the merge of the mesolophid and the metalophid, and at its labial end it would not be located the ectostylid but the protoconid, which would be situated a little more labially than the hypoconid, as in the p4. Then, the second crest would be an accessory structure different from the anterior cingulum, non homologous to any one of the molars or of the primitive dp4s.

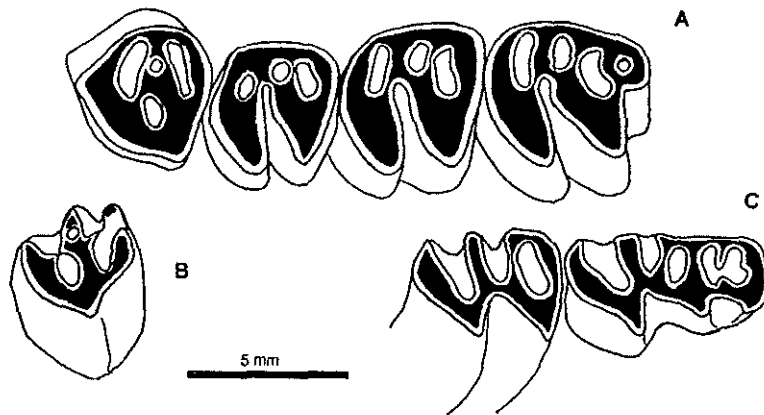


Figure 9.— *Luantus* sp. A: left P4-M3. B: left little worn P4. C: right dp4 -m1.



An incipient accessory crest between anterolophid and metalophid is also observed in *Luantus* (figure 9 B) and in *Neoreomys*: the anterior fossetid is frequently crossed by a crest, generally incomplete, extending transversally between both rami of the anterolophid. In *Scleromys* and *Cuniculus* a complete transverse crest is observed at this position, and in *Dasyprocta* there are as many as two accessory crests. The homologies interpretation given by Patterson and Wood (1982) points out that also in *Cephalomys* the dp4 has a transverse structure anterior to the protoconid and metaconid, different from the anterolophid and, as in *Soriamys*, there is not a recognizable mesolophid.

Therefore, the pentalophdnty of the dp4 of *Soriamys*, as well as that of *Cephalomys*, would be a derived character, result of the fusion of metalophid and mesolophid and the development of a new crest inserted between the anterolophid and the metalophid. This hypothesis is preferable because it is coherent with the evolutionary degree of the remaining dentition and with the observations in other protohypsodont genera.

If these interpretations are correct, what we initially considered as the ectolophid in the dp4 of *Soriamys*, would be a new longitudinal element extending anteriorly to the metalophid, probably an anterior derivation of the ectolophid. This structure is also present in the dp4 of *Luantus* (Figure 9 B) and *Cephalomys*.

*Soriamys ganganensis* nov. sp.

(figures 10 to 12)

**Etymology:** From Pampa de Gan Gan, Chubut province, locality from which proceed all the known materials.

**Holotype:** MACN CH 1765, a complete skull with articulated jaw.

**Hipodigma:** The holotype and MACN CH 1766, an anterior portion of skull with complete upper dentition; MACN CH 606, a complete palate with the dentition and CNP PV 1988-3, a portion of a right jaw with m1 and m2.

**Stratigraphic provenance and age:** Sarmiento Formation (Bown and Fleagle, 1993). Colhuehuapian Age. (Early Miocene) (Flynn and Swisher 1995).

**Geographic provenance:** Pampa de Gan Gan, next to Cerro Sacanana (Rusconi 1935; Feruglio, 1949; Hershkovitz 1974, Fleagle and Bown 1983), center-north of Chubut province, Argentina (figure 1).

**Diagnosis:** Jugal teeth more hypsodont and slightly bigger than those of *S. gaimanensis*. Occlusal morphology simplified in earlier stages of wear. Abundant cement. Enamel absent on the labial margins and on the posterolabial corners of the slightly worn upper teeth. M3 trilobated until more advanced stages of wear than *S. gaimanensis*.

**Description**

The specimen MACN CH 1765 (figure 10) is a very well preserved and articulated skull and jaw, with part of the first vertebrae articulated. The anterior end of

the rostrum and the posterior end of the angular process are incomplete.

The skull is low and long. The cranial roof is flat, slightly depressed at the interorbital region. The rostrum and the brow are narrow, the parietal region is rather broad. The orbit and the bulla are moderately large and rounded.

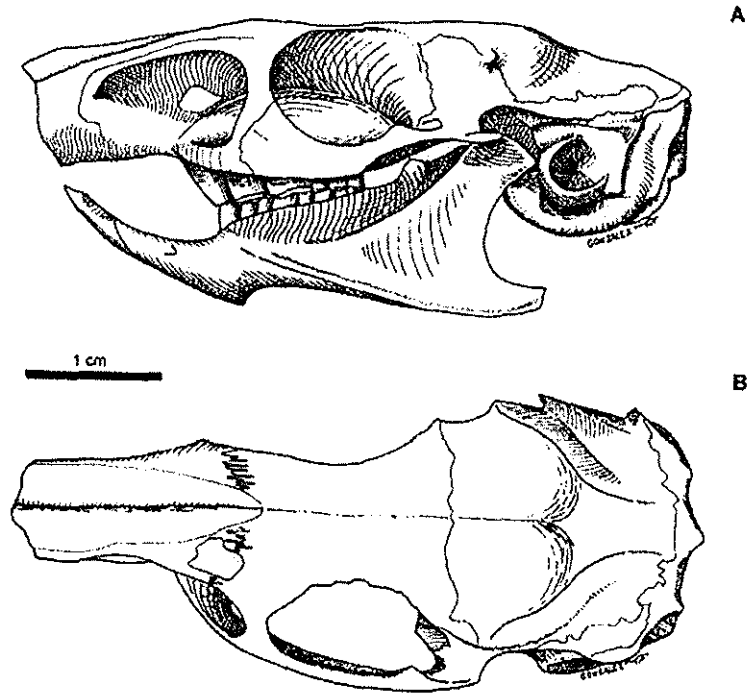


Figure 10.— *Soriamys ganganensis* sp. nov. A: MACN CH 1765 (holotype) complete skull and jaw in lateral view. B: idem, in dorsal view.

The rostrum is long, almost cylindrical. The nasals are narrow penetrating deeply between the frontals, unlike *Perimys*, *Cephalomys* and chinchillids.

The lateral wall of the rostrum is mostly occupied by the masseteric fossa. It has an ogival contour and it is well developed; its dorsal limit is formed by a prominent rim of the maxillary, as in *Lagostomus*, *Chinchilla*, *Perimys* and *Cephalomys*, but more prominent than in *Abrocoma* and *Lagidium*. The anterior portion of the fossa is deeper and lacks a well marked anterior margin, present in *Dasyprocta* and *Lagostomus*. The incisor is excluded of the masseteric fossa like in *Chinchilla*. The ventrolateral wall of the rostrum is almost plane, excepting the tuberosity of the alveolus of the incisor. The premaxillary-maxillary suture turns forward, as in *Lagidium* and *Chinchilla*; as in the last genus the premaxillary is completely excluded of the masseteric fossa. The ascending process of the premaxillary is long and narrow; it extends backwards almost reaching the level of the dorsal root of the zygoma, but unlike the chinchillids the process is shorter than the nasals. This process has not a groove for nervous passage, seen in *Perimys*, *Dasyprocta*, *Neoreomys* and probably in *Cephalomys*.

The rostral opening of the lacrimal channel is large, elliptic and it is located on the

lateral wall of the rostrum, slightly above the ventral root of the zygoma, like in *Cephalomys*. On the contrary, in *Perimys*, *Abrocoma* and cavioids this opening is more dorsally located, being more posterior in chinchillids.

The frontals are narrow, slightly depressed and as long as the nasals; they do not penetrate between the nasal and the premaxillary, unlike *Abrocoma* and *Perimys*, and it is impossible to distinguish whether the frontals penetrate between the premaxillary and the maxillary, as in chinchillids, *Abrocoma*, *Octodontomys* and *Cephalomys*. The interorbital strait of the frontals is little marked. The supraorbital rim is little prominent and scarcely curved, giving a circular contour to the orbit. The supraorbital border continues anteriorly with the posterior margin of the dorsal root of the zygoma, as in almost all the cavioids, *Lagidium* and *Perimys*, without a developed lacrimal notch. The rim is incomplete at the level of the postorbital process of the frontal, although it seems to have been not well developed.

The dorsal root of the zygoma is strong and it is located at the level of the M2. The lacrimal bone must have been restricted to the posterior margin of the dorsal root, but the delimiting sutures can not be distinguished clearly. The dorsal root is differentiated from the vertical ramus of the zygoma by a marked strait of the maxillary. The vertical ramus widens gradually downwards, converging with the ventral root and the horizontal ramus, giving rise to the strongest portion of the zygomatic arch.

The ventral root is dorsally plane, sloping backward and lacks the groove for passage of the infraorbital nerve. The anterior border of the root is situated slightly before the P4, and the posterior border is between the alveoli of the P4 and the M1. The ventral root is located very low, near the alveolar border. The anterior face of the root is almost vertical, its height is constant and it is continuous to the anterior border of the vertical ramus. The disposition and extension of both roots coincides with those of *Cephalomys*, although in the latter the ventral root is dorsally convex. In *Octodon* and *Abrocoma* the vertical ramus is more slender and both roots are placed more anteriorly. In chinchillids and *Perimys* the dorsal root is located posteriorly, at the level of the M3. In frontal view, the ventral root of *S. ganganensis* projects slightly ventrally, not horizontally as in *Cephalomys*. On the ventral face there is a fossa for the origin of the *M. masseter superficialis* (Woods and Howland, 1979), it is little extended, subcircular in outline, anteromedially well limited, and deeper than that of any other compared genus.

The horizontal ramus of the zygoma is low and narrow, forming an arch from the ventral root up to the suture with the squamosal, extending more ventrally than the alveolar border, as in cavioids, *Dasyprocta*, *Neoreomys* and *Chinchilla*. In dorsal view, the zygoma is nearly parallel to the anteroposterior axis of the skull. The ascending process of the yugal forms a portion of the vertical branch, but it does not reach the lacrimal, as in *Lagostomus*. The ventral surface of the yugal shows a shallow lateral jugal fossa as in *Lagostomus*. The posterior end of the yugal and the anterior part of the squamosal form a small dorsal process, limiting the orbit posteroventrally. The zygomatic portion of the squamosal is relatively long and forms an inflection less pronounced than in *Perimys* and *Lagostomus*, but more than in *Abrocoma*.

The orbital cavity is large and deep. The anterior margin of the orbit is semicircular. The posterior margin is not much defined, as in *Octodon*, *Abrocoma* and

*Neoreomys*. The orbital portion of the maxillary is high and globosous, as in the Chinchillinae.

The squamosal is almost excluded of the posterior wall of the orbit, as in *Octodon* and *Abrocoma*. Behind the orbit, a small and acute postorbital process of the squamosal is located just on the descendent portion of the parieto - squamosal suture, similar to *Octodon*.

The posterior process of the squamosal is very narrow behind the glenoid cavity, and forms a crest that determines the lower temporal line, as in chinchillids, *Abrocoma*, *Echimys* and *Myocastor*. Above the MAE (*meatus acusticus externus*) the squamosal turns nearly plane and wide; the suture with the parietal is crenulated up to the parietal foramen. Behind it, the squamosal is horizontal, forming part of the cranial roof.

The parietal region is broad and mostly flat. The fronto-parietal suture is straight and transverse. The parietals are longer than frontals; their anterior portion are slightly globosous, with a little medial depression; backwards they turn plane, and together with the posterior processes of the squamosals, they are disposed in a single horizontal plane, as in *Lagostomus* and *Myocastor*.

The parietal crests are lyre shaped and do not converge on the medial line, as in Chinchillinae, *Abrocoma*, *Octodontomys*, and in lesser degree in *Ctenomys* and *Microcavia*. The crests do not reach the posterior margin of the parietals, but they break off just where the parietals turn plane. Behind this point, there is a medial globosity, as in *Echimys*, *Coendou* and *Galea*, limited by two faint lateral grooves that seem to be the continuations of both parietal crests. There is no evidence of the sagittal crest.

The parieto-occipital suture is transverse and straight in the medial portion, and very crenulated on the flanks. The supraoccipital is confined to the posterior border of the cranial roof and does not penetrate between the parietal and the squamosal. On its posterior margin, the supraoccipital has two notches at each side of the medial occipital crest, that correspond to the respective fossae of the occiput.

The lateral process of the supraoccipital extends on the sides of the skull only up to the dorsal margin of the bulla, as in *Abrocoma*, *Perimys*, *Lagidium* and *Chinchilla*, and separates the squamosal and the mastoid, unlike the cavioids and dasyproctids. The proximal portion of the process is very slender, it widens distally and projects backwards, penetrating between the squamosal and the dorsal margin of the bulla. This particular disposition is not present in any other compared taxa. The posterior margin of the process is prominent and laps over the mastoid processes, forming the lambdoid crest; the latter is arched and continues ventrolaterally on the surface of the bulla up to the level of the stylomastoid foramen, forming at its ventral end a small apophysis for the articulation of the thympanohial.

The bulla is large, well rounded, lengthened anteroposteriorly and the rear is gradually compressed. The MAE is in middle of the bulla, slightly displaced toward the dorsal margin, so the sinus epitympanicus is reduced. In front of the latter there is a postglenoid foramen, as small as in *Lagostomus* and much smaller than in the Chinchillinae, *Perimys* and *Abrocoma*.

The MAE is large, but not as much as in the Chinchillinae and *Abrocoma*, circular in shape, and limited by a lip, more prominent on the anteroventral border and

absent on the posterodorsal border. This lip is not tubiform, as it is in chinchillids. As in *Perimys* and chinchillids, there is an accessory orifice just below the MAE, from which it is isolated by the lip. Such orifice is almost imperceptible in *Abrocoma* and *Octodontomys*.

The mastoid is large and inflated; it forms the posterolateral angle of the skull, so it is visible in lateral as well as in posterior view. It extends dorsally exceeding the level of the dorsal margin of the bulla, and reaching the cranial roof. The mastoid penetrates between the lateral process of the supraoccipital and the exoccipital, excluding the latter of the posterior margin of the lateral wall of the skull. This disposition differs from that of *Lagostomus* because in this genus the mastoid is exposed mainly on the occipital plane. It also differs from that of *Perimys*, in which the mastoid is concave and excluded from the posterior wall of the skull. In the Chinchillinae, *Abrocoma*, *Octodon* and *Octodontomys* the mastoid is much more inflated, but in these three genera this feature would be closely related to the enormous expansion of the bulla. The development of the mastoid in *Soriamys* is similar to that of caviids, in which the bulla is middle sized but the mastoid is conspicuous and has an important participation in the lateral wall of the braincase.

The occiput of *Soriamys* is vertical, rather low and wide. The occipital crest is prominent, more acute in the dorsal portion. The presence of part of the first vertebrae articulated to the skull hides the condyles and the foramen magnum. The exoccipitals form both protuberances on the dorsolateral angles of the occiput. Two deep occipital fossae are delimited dorsolaterally by these protuberances, and medially by the occipital crest. The fossae are disposed diagonally toward the base of the paraoccipital apophysis, as in *Perimys*. Only the proximal portion of the left paraoccipital apophysis is preserved: it is small, almost cylindrical in section and, unlike *Lagostomus* and *Perimys*, it is curved forwards following the posterior surface of the bulla, to which it is leaned against.

The features of the palate can be seen in MACN CH 606 (figure 11 A) and 1766.

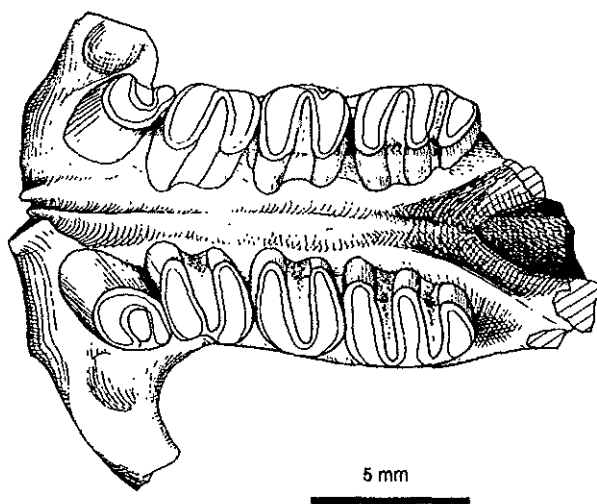


Figure 11.— *Soriamys ganganensis* sp. nov. MACN CH 1766, palate with complete dentition.

The incisive foramina are large, at least the preserved parts. They extend backward up to the base of the premolars and continue as a faint palatal groove between the teeth rows. There is a slight difference in height between the diastema and the palate, as in *Perimys* and *Cephalomys*. The maxillary fossae are moderately developed. The teeth rows are very close and, diverging gently posteriorly, so the palate is very narrow as in *Geocapromys* and *Abrocoma*. The anterior portion of the palate, between the premolars, is slightly wider than between the M1s, due to the reduced transverse diameter of the P4s. There is a faint medial palatal crest, less prominent than in chinchillids, which is absent in *Cephalomys* and *Abrocoma*.

In MACN CH 606 the palate is slightly convex between the M2, perhaps due to the deformation, although this condition is also insinuated in MACN CH 1766. The real extension of the palatines cannot distinguish; they are strongly depressed only between the M3s. This feature resembles the palate of chinchillids and *Perimys*, though the palatines of *Soriamys*, on the contrary, constitute a triangular platform above the palate level and just before the choanes. The choanes are elliptic in outline, and penetrate the palate up to the third lobe of the M3 and have an. This palate is atypical among caviomorphs. It may be interpreted that this morphology derives from a concave and triangular palate, as that of *Perimys* or *Chinchilla*, that has suffered a secondary compression, returning to a primitive parallel disposition of the teeth rows, but remaining only a vestigial concavity in its posterior portion.

MACN CH 1765 (figure 10 A) has both mandibular rami articulated to the skull, though the left one is better preserved. CNP PV 1988-3 is a jaw fragment poorly preserved with the m1 and m2.

The diastema is long (as much as the teeth row), cylindrical and gently curved as in *Chinchilla* and *Eocardia*. Ventrally it has a mental keel located below the p4. The diastema is little concave, so its dorsal surface is almost in the same plane of the alveolar line, as in *Cephalomys*, *Eocardia* and most of the caviids. The mental foramen opens on the dorsolateral surface, as in *Prolagostomus*, *Lagidium* and *Cavia*, and its position is unusually anterior, even more than in *Eocardia* and the Chinchillinae. As in *Cephalomys*, but unlike chinchillids, *Perimys* and *Abrocoma* no vascular foramina can be seen over the ventral mental surface.

The fossa for insertion of the tendon of *M. masseter medialis pars infraorbitalis* (Woods and Howland 1979) is situated over the external face of the jaw very anteriorly, below the p4 as in *Cephalomys*, *Lagidium* and *Abrocoma*. In opposition to the latter, *Octodontomys* and *Ctenomys*, the ventral margin of this fossa continues the masseteric crest. The masseteric crest is very prominent and low, extending backwards forming all the ventrolateral margin of the jaw, so the angular region is extroverted. This character separates *Soriamys* from *Perimys*, *Cephalomys* and all the cavioids and chinchillids, and resembles octodontoids and erethizontoids. The end of the angular process is incomplete, but the preserved part suggests that it extended more ventrally than the mental keel and more posteriorly than the postcondylar process, as in *Cephalomys* and *Neoreomys*, but not as much as in caviids and eocardiids.

There is a deep lateral fossa for the insertion of the *M. masseter medialis pars zygomatico-mandibularis* (Woods and Howland 1979), ventral to the coronoid process, extending from the central region of the jaw to the ascending ramus, near the condyle.

This fossa is also present in *Cephalomys*, *Perimys* and in all the cavioids and chinchillids, but it is very reduced in *Abrocoma*. The coronoid process is preserved only in the base, but it seems to have been not very developed. The ascending ramus is rather low, but not as much as in *Cephalomys* and caviids. The condyle is ovoid, and rather compressed. The postcondylar process is well developed. The posterior border of the jaw is low-necked, but less than *Abrocoma* and *Chinchilla*. None of the available specimens of *Perimys* and *Cephalomys* has this part of the jaw preserved.

Upper complete dentition is seen in the specimens MACN CH 606 (figure 11 and 12 C) and MACN CH 1766 (figure 12 B). The articulated jaw in the type specimen (MACN CH 1765) only allows to see the left P4 and M1 and part of the M2 and M3 of the same side (figure 12 A). The lower dentition is known by the m1 and m2 insert in the jaw fragment CNP PV 1989-3. In the holotype can only be observed the occlusal surface of the right p4, because both lower teeth rows are hidden under the palate.

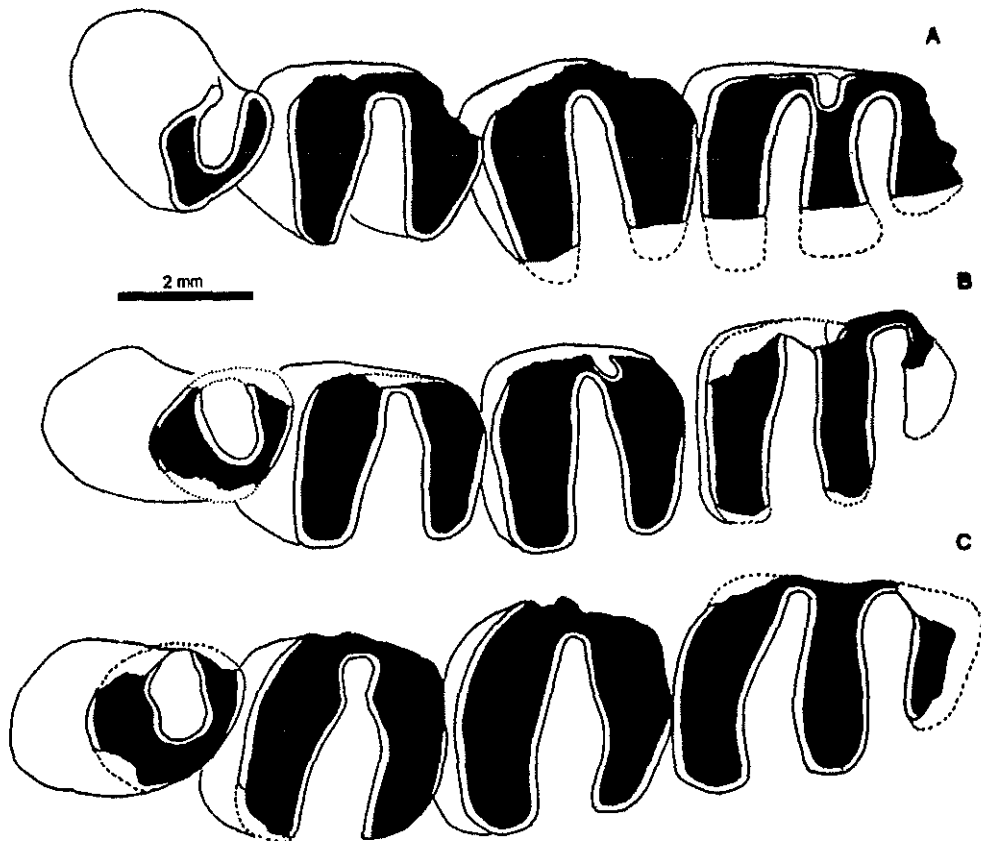


Figure 12.— *Soriamys ganganensis* sp. nov. Upper left complete dentition. A: MACN CH 1765 (holotype). B: MACN CH 1766. C: MACN CH 606.

Teeth are very high crowned but rooted. The cement is more abundant than in *S. gaimanansis*, filling almost completely the valleys. In the upper teeth the wear is very conspicuous on the posterolabial margins and on the lingual apices. The enamel seems to be absent on the labial faces and on the posterolabial corners of the worn upper teeth.

In CNP PV 1989-3 the enamel is absent on the base of the anterior wall and on the posterolingual corners of m1 and m2. The teeth are slightly bigger than those of the type species (see tables 1 and 3).

The P4 is unilobated, nearly cylindrical, with the base strongly curved forwards. Unlike *Perimys* and *Cephalomys*, the occlusal surface is very small, less than half the surface of the M1, and is even lesser in the juvenile holotype. In this specimen (figure 12 A) the premolar is little worn, so the occlusal surface is still subtriangular. There are two crests that diverge from the lingual corner, as in *S. gaimanensis*. The anterior crest does not reach the labial border, but from its end it starts another slender crest that extends to a small labial tubercle (the paracone), completing the anterior margin of the tooth. The posterior crest constitute the whole posterior margin, it is gently concave forwards, thicker at its labial portion (where the metacone should be located). Paracone and metacone are very close, related by a thin anteroposterior crest. The central valley is U-shaped and is still open on the buccal side in the type specimen. As in the species from Gaiman, there is no evidence of a differentiated hypocone-hypoflexus. In the remaining specimens the central valley is closed lingually, so a more advanced stage of wear is deduced, and the anterior crest turns thicker than the posterior.

The M1 and M2 are composed of two subequal prisms, with subtriangular section but with rounded lingual apexes. In both teeth the transverse diameter of the anterior prism is larger than the posterior. The prisms are united by a thin labial isthmus. The hypoflexus is transversal, very wide and penetrating, with its walls nearly parallel. There is a minute flexus on the labial margin, near the isthmus, of the second prism of the M2 and the M3 of MACN CH 1766, and on the M3 of the holotype (this region is not preserved in the M2 of the holotype). This flexus may be homologous with the mesofossette of *S. gaimanensis* in a vestigial state, because it is the more persistent flexus and has the same location.

The M3 is composed of three prisms: the two anterior prisms have nearly the same shape and size than those of M1 and M2; the third prism is transversally shorter and, unlike *S. gaimanensis*, the lingual end remains separated from the second lobe probably in every stage of wear.

In the adult specimens, the contour of the prisms is irregular and sinuous, specially in the MACN CH 606 (figure 11 B).

The occlusal surface of the p4 is hardly visible in the right jaw of MACN CH 1765; however, a trilophodont pattern can be distinguished, as in *S. gaimanensis*.

The m1 and m2 of CNP PV 1989-3 are different from those of *S. gaimanensis* only in the greater amount of cement among the crests.

The lower incisors are thin and have anteroventral convex face. They extend into the jaw up to the level of the m2, as in *Chinchilla*, *Eocardia* and *Cavia*, but they are longer than in *Lagidium*, *Perimys* and *Dolichotis*.



## DISCUSSION

The generic identity of the described species is based upon the remarkable similarity of their lower dentitions and the suggestive likeness of the young upper dentition of the species of Gan Gan with the adult upper dentition of the species of Gaiman. However, the taxon from Gan Gan differs from that of Gaiman in the following features:

- more abundant cement
- earlier simplification of the occlusal morphology
- more heterogeneous distribution of the enamel
- more persistence of the third lobe of the M3

All the mentioned differences are related to a higher degree of hypsodonty of *S. ganganensis*. The differences between both taxa are quantitative, but large enough to justify a differentiation at specific level. This two species are representative of a single phyletic line in different stages of development of the hypsodonty.

The phylogenetical relationships of *Soriamys* with other caviomorphs are really complex: the lower dentition shares characters with such unrelated genera as *Cephalomys*, *Echimys* and *Abrocoma*, while the upper dentition resembles *Perimys* and the eocardiids, depending on the stage of wear.

We consider that *Soriamys* is best classified among the chinchilloids because it shows the following derived characters:

- laminar hypsodont teeth with cement (at least in advanced stages of wear)
- development of a third lobe in the M3 due to the persistence of the brachyflexus
- jugal with ascending process (Glanz and Anderson 1990; Walton 1990).
- concave palate, at least at its posterior portion.
- very prominent dorsal rim of the rostral masseteric fossa
- mandibular fossa for the insertion of the *M. masseter medialis pars zigomaticomandibularis* very developed

In order to evaluate the phylogenetical relationships among *Soriamys* and the remaining chinchilloids (including *Abrocoma*), a cladistic analysis was performed using the implicit enumeration option (i.e.) of the Hennig '86 program. Forty-five cranial, mandibular and dental character were selected (see Table 4) for the analysis. To establish the character polarities we selected *Steiromys* as the outgroup by virtue of previous hypothesis that suggest that erethizontids are the more plesiomorphic group among the caviomorphs (Sarich and Cronin, 1980; Woods and Hermanson, 1985; Bugge, 1985; Bryant and McKena, 1995). However, premolar characters were polarized by comparing with *Gaudeamus*, *Platypittamys* and *Sallamys*, assuming that the highly molarized premolars of the erethizontids is not the ancestral condition for the remaining caviomorphs (Patterson and Wood, 1982). *Octodontomys* (octodontid) and *Proechimys* (echimyid) was also included in the analysis to evaluate the affinity of *Abrocoma* with

the octodontoids

A single most parsimonious tree (figure 13) was obtained, with length=120, ci=54 and ri=57. *Soriamys* and *Cephalomys* cluster in a monophyletic group (the Cephalomyidae) supported by five sinapomorphies: low condyle (character 28), angular process extends more ventrally than the mental keel (character 30), dorsal surface of the diastema is almost in the same plane of the alveolar line (character 34) and asymmetrical dental pattern (character 43). Moreover, *Soriamys* and *Cephalomys* share the fusion of the anterolophid and mesolophid in the lower teeth, the presence of an accessory transverse crest and an anterior derivation of the ectolophid in the dp4, although these characters were excluded from the cladistic analysis because they can not be evaluated in most of the taxa. There is a reversion from an euhypsodont to a protohypsodont condition at this node (character 37[2]), which phylogenetical meaning is dubious. The affinities with *Cephalomys* may indicate that *Soriamys* corresponds to a group of early hypsodont forms, already recognized by Loomis (1914), Miller and Gidley (1918), Landry (1957) and Vucetich (1985), but each one with different criteria about its concept and the content (see in Wood and Patterson, 1959; Vucetich, 1985). Among the genera traditionally referred to the Cephalomyidae, only *Cephalomyopsis* and probably *Litodontomys* have also an asymmetric dental pattern and also may be included in the Cephalomyidae.

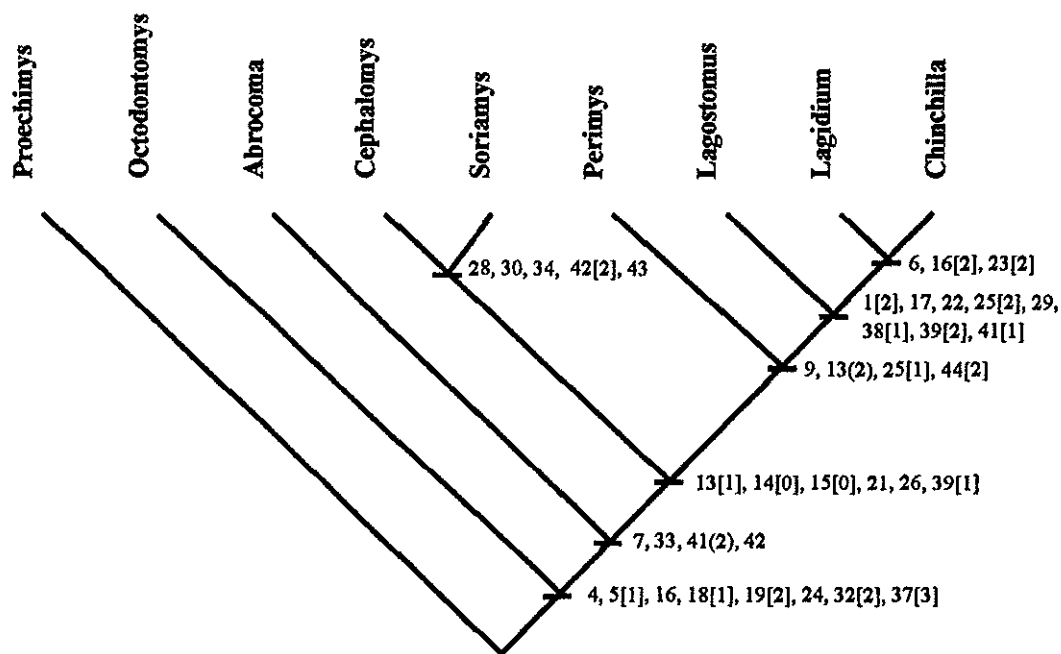


Figure 13.— Most parsimonious tree resulting from an exhaustive search. Length=120, ci=54 and ri=57. Identical topology is obtained if *Proechimys* is replaced by *Eumysops*, *Eurozygomatomys* or *Myocastor*.

On the other hand, *Perimys* clusters with the chinchillids on the basis of four sinapomorphies: the laminar dental pattern (character 44[2]), the divergence of the tooth rows (character 9), the relative position of the dorsal root of the zygoma

(character 13[2]), and the incipient development of a tubiform MAE directed posterodorsally (character 25[1]). "*Scotaeumys*" is a juvenile specimen referable to *Prolagostomus* (Vucetich and Verzi, 1993) or some other related genus. *Scotamys* was excluded from the analysis because the majority of the characters can not be evaluated in this genus. *Scotamys* would be more related to *Perimys* because it shows the same dental pattern, with interlaminae cement and the hypoflexus penetrating diagonally against the parafossette (not transversally opposed to the protoloph). According to the interpretation of Wood and Patterson (1959), *Scotamys* already has a very molarized P4, with a differentiated hypoflexus, as in *Eoviscaccia* and the later chinchillids, so its affinity with the chinchillids could be closer than with *Perimys*. However, the specimen illustrated by these authors (M.N.H.N.1903-3-8, page 314, figure 8 A) seems to be a right P4 instead of a left one, because the base of the premolar normally curves anterolabially (Vucetich, pers. com.). Following this reinterpretation, the large central valley of this specimen would be the paraflexus opening on the anterolingual margin and it would have not a differentiated hypoflexus; the interruption of the enamel occurs mainly on the posterior border, just like in the upper molars. *Scotamys* and *Perimys* would be representatives of a lineage distinct of the Cephalomyidae, perhaps the Neoeplemidae (Kraglievich, 1926; Bondesio *et al.*, 1975) or Perimyidae (Landry, 1957), more closely related to the chinchillids than to the cephalomyids.

Cephalomyids are the sister group of the remaining chinchilloids. This relationship is supported by six sinapomorphies: the relative position of the dorsal root of the zygoma (character 13[1]), the reduction of the lateral process of the supraoccipital (character 21), the presence of a conspicuous accessory orifice just below the MAE (character 26), the high degree of penetration of the hypoflexus in the upper molars (character 39[1]), the participation of the jugal bone in the vertical ramus of the zygoma (character 14[0]) and the reduction of the lateral jugal fossa (character 15[0]). However, these osteological features can be evaluated only in *Soriamys*.

*Abrocoma* was traditionally considered as related to the octodontoids (Ellerman, 1940; Simpson, 1945; Landry, 1957; Patterson and Wood, 1982; Carleton, 1984; Reig, 1986); in fact, the middle ear morphology (Parent 1980) enamel microstructure (Martin, 1992) and the zygomasseteric and mandibular structure of *Abrocoma* correspond to those of the octodontoids. However, this genus also presents the mentioned asymmetric dental pattern; the disposition of crests of lower teeth is similar to *Soriamys*, while the "8" shape of the uppers resembles *Cephalomys*. Above we have suggested that the asymmetric dental pattern could be more related to similar masticatory requirements than to phylogenetic affinities, but in the case of *Abrocoma* this character is associated with many other features shared with the chinchilloids, already pointed out by Glanz and Anderson (1990). In the current analysis *Abrocoma* clusters with the chinchilloids by sharing four synapomorphies: the presence of the rostral opening of the lacrimal channel (character 7), the disposition of the lophos like transverse laminae intercalated with thick deposits of cement (character 41) (after Glanz and Anderson, *op. cit.*), the elongated, cylindrical and nearly horizontal sinfisiary region of the jaw (character 33), and the presence of a third lamina on the M3 (character 42), although probably originated by a mechanism different from that of the chinchilloids. Thus, the asymmetric dental pattern in *Abrocoma* may suggest some degree of affinity to the cephalomyids. It is really a problematic genus and its affinities are still controversial.

The controversy of this genus is reflected by the fact that *Octodontomys* and *Proechimys* do not cluster in our analysis as it would be expected; identical results are obtained if *Proechimys* is replaced by *Eumysops*, *Eurozygomatomys* or *Myocastor*. Only if *Abrocoma* is replaced by *Ctenomys*, then the later groups with *Octodontomys*, and both with *Proechimys*, and do not change the relationships among the remaining taxa (figure 14).

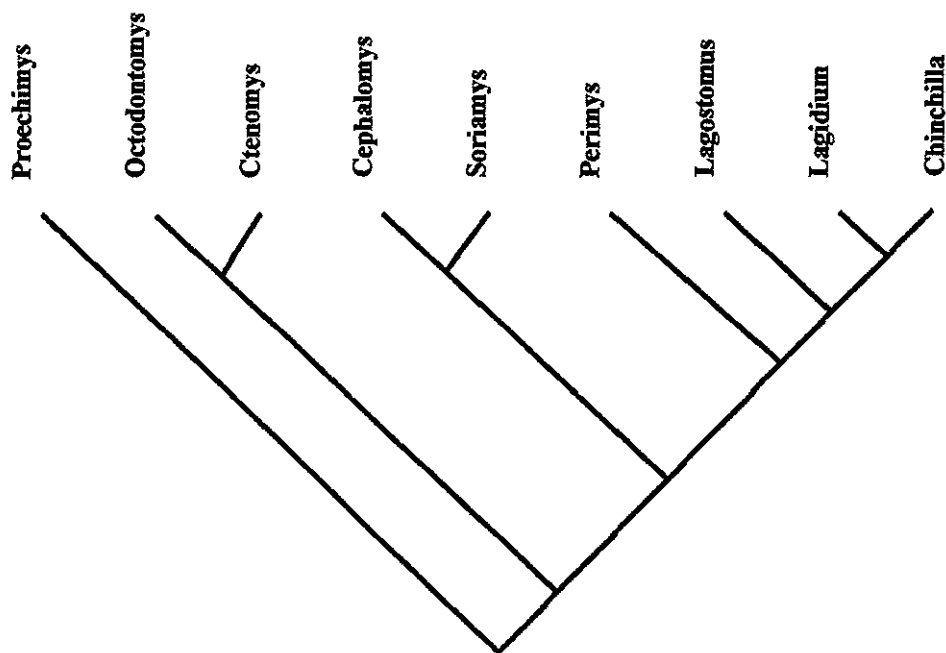


Figure 14.— Most parsimonious tree resulting from an exhaustive search replacing *Abrocoma* by *Ctenomys*. Length=117, ci=55 and ri=59.

On the other hand, *Soriamys* and *Cephalomys* share with the eocardiids some suggestive dental characters, as the transversal penetration of the hypoflexus of the upper molars and the development of an anterior derivation of the ectolophid in the dp4. Moreover, the mandibular design of *Soriamys* resembles that of the eocardiids, caviids and hydrochoerids: low mandibular ramus, slender and gently curved sinfisiary region, low condyle and angular process ventrally directed. However, in the cephalomyids the ventral position of the masseteric crest is retained, and the lateral extroversion of the angular region persists in *Soriamys*. These suggestive similarities must not be interpreted necessarily as an evidence of a particular affinity between cavioids and cephalomyids, as was proposed by Kraglievich (1940), followed by Simpson (1945), and McKenna and Bell (1998), but the cavioids and chinchilloids as a whole. This hypothesis is concordant with the proposal of Martin (1992) upon the enamel microstructure and that of Bryant and McKenna (1995) based on comparisons of the anatomy of the middle ear in living and fossil species.

## CONCLUSIONS

Both species described in this paper, *Soriamys gaimanansis* and *Soriamys ganganensis*, are representatives of a single phyletic line in different stages of development of the hypsodonty.

*Soriamys* is a chinchilloid allied to *Cephalomys*, and both integrate a natural group, the Cephalomyidae, with proper dental characters, like the asymmetry between the occlusal morphology of the upper and lower teeth. *Cephalomyopsis*, and probably also *Litodontomys*, may be considered part of this clade. *Scotamys* and *Perimys* represent a distinct lineage, more closely related to the Chinchillidae.

Numerous osteological and dental characters shared by *Soriamys*, *Cephalomys* and the eocardiids and caviids suggest that the relationships between the Cephalomyidae and the Caviioidea are closer than what was traditionally proposed, perhaps as a consequence of a larger affinities of chinchilloids and cavioids as a whole. *Abrocoma* may represent a collateral branch early differentiated from the chinchilloid stock, but its relations to the cephalomyids, neopiblemids and chinchillids are still uncertain. Thus, its correct interpretation will only be attained through a more extensive study including all the caviomorph superfamilies, which is far beyond the objectives of the present work.

The Cephalomyidae seems to have been the more important group of high-crowned caviomorph rodents from the Deseadan to the Colhuehuapian, on the basis of its abundance (*Cephalomys* is the most abundant rodent of the Deseadan record of Patagonia, *Soriamys* is the most abundant hypsodont rodent, at least in the colhuehuapian Gaiman locality) and its diversity, (*Cephalomys* and *Litodontomys* in the Deseadan and *Cephalomyopsis* and *Soriamys* in the Colhuehuapian). The cephalomyids would have declined before the Santacrucian, coinciding with the adaptive radiation of other high-crowned caviomorph rodents, as the caviids, dasyproctids and, to a lesser extent, the chinchillids.

It is necessary to point out that, although the two localities (Gaiman and Gan Gan) have been referred to the Colhuehuapian age, the more advanced evolutionary stage of the species from Gan Gan may indicate a younger age. On the contrary, the record of *Acdeston* in Gan Gan (Bown and Fleagle, 1993) seems to suggest the opposite. No statement based on so few taxa can be sustained, and only further study of other members of the rich fauna of Gan Gan will allow us to clarify its relative antiquity.

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TABLES 1 - 5

		P4	M1-2	M3	DP4	p4	m1	m2	m3	dp4
	<i>n</i>	5	14	9	2	6	9	9	4	2
AD	x	2.02	2.78	3.28	2.68	2.63	2.72	3.34	3.56	2.93
	SD	0.09	0.24	0.23	0.18	0.34	0.26	0.13	0.09	0.11
ATD	x	-	2.21	2.65	1.70	1.73	1.93	2.54	2.69	1.35
	SD	-	0.27	0.17	0.07	0.35	0.28	0.19	0.10	0.00
PTD	x	2.30	2.08	2.37	1.58	2.14	2.03	2.60	2.59	1.65
	SD	0.15	0.34	0.14	0.04	0.32	0.29	0.17	0.10	0.00

AD = Anteroposterior diameter  
 ATD = Anterior transverse diameter  
 PTD = Posterior transverse diameter  
*n* = Number of specimens  
 x = average  
 SD = Standard deviation  
 M1-2= M1 or M2

Table 1.— Summary of tooth measurements of *Soriamys gaimanensis* gen. et sp. nov. (in mm).

	MACN CH 1765	MACN CH 1766	MACN CH 606
Skull length	5.63	-	-
Interorbital width	1.27	-	-
Rostrum width	0.79	-	0.88
Rostrum height	0.88	-	1.21
Vertical diameter of the orbit	1.13	-	-
Anteropost. diameter of the orbit	1.26	-	-
Occipital width	1.68	-	-
Maximum parietal width	1.98	-	-
Diameter of the MAE	0.37	-	-
Height of the bulla	1.02	-	-
Infraorbital foramen height	0.69	-	0.98
Infraorbital foramen width	0.52	-	-
upper alveolar line length	1.54	1.5	1.51
Palate width between P4s	-	0.29	0.27
Palate width between M2s	-	0.18	0.21
Palate width between post. lobe of M3s	-	0.39	0.43
Palate length	-	1.49	1.44
Choanes width	-	-	0.33
Preserved length of the jaw	3.68	-	-
Ramus depth at p4	0.56	-	-
Ramus depth at m3	1.25	-	-
Vertical ramus depth (at condyle)	1.58	-	-
Diastema length	0.92	-	-

Table 2.— Cranial and mandibular measurements of *Soriamys gaimanensis* gen. et sp. nov. (in mm).

Collection number	tooth	anterop. diameter	anterior transv. diameter	post. transv. diameter
MACN CH 606	right P4	-	0.231	-
"	right M1	0.32	0.283	-
"	left M1	0.299	0.301	-
"	right M2	0.312	0.34	-
"	left M2	0.314	0.337	-
"	right M3	0.457	0.347	-
"	left M3	0.465	0.301	-
MACN CH 1765	left P4	-	-	0.196
"	left M1	0.297	0.263	-
"	left M2	0.314	-	-
"	left M3	0.415	-	-
MACN CH 1766	right M1	0.265	0.266	-
"	left M1	0.282	0.25	-
MACN CH 1766	right M2	0.288	0.31	-
"	left M2	0.296	0.306	-
"	right M3	0.43	-	-
"	left M3	0.422	0.303	-
CNP PV 1988-3	right m1	0.303	-	-
"	left m2	0.322	0.255	-

Table 3.— Dental measurements of *Soriamys gaimanensis* gen. et sp. nov. (in mm).

Table 4.— List of characters and character states

Character 1. Posterior extension of the premaxillaries in relation to the nasals

0=shorter 1=equals 2=longer

Character 2. Penetration of the frontals between nasals and premaxillaries

0=absent 1=present

Character 3. Groove for nervous passage on the ascending process of the premaxillary

0=absent 1=present

Character 4. Incisor excluded from the masseteric fossa

0=no 1=yes

Character 5. Premaxillary excluded from the masseteric fossa

0= not excluded 1= partially excluded 2= completely excluded

Character 6. Maxillary-premaxillary suture turns forward

0= no 1=yes

Character 7. Rostral opening of the nasolacrimal channel

0= absent 1= present

Character 8. Exposition of the lacrimal bone on the vertical ramus of the zygoma

0=small 1=big

Character 9. Divergence of the tooth rows

0=subparallel 1=slightly divergent 2=very divergent

Character 10. Concavity the palate

0= plane 1= concave

Character 11. Horizontal ramus of the zygoma extends more ventrally than the alveolar border

0= no 1= yes

Character 12. Groove on the maxillary for passage of the infraorbital nerve

0= absent 1= shallow 2= deep

Character 13. Relative position of the dorsal root of the zygoma

0= before the level of the m1 1= between m1 and m2 2= behind the level of m2

Character 14. Jugal excluded from the vertical ramus of the zygoma

0= not excluded 1= partially excluded 2= completely excluded

Character 15. Ventrolateral jugal fossa

0= absent 1= present

Character 16. Frontals penetrate between parietals

0= no 1= yes

Character 17. Supraoccipital penetrates between parietal and squamosal

0= no 1= yes

Character 18. Dorsal extension of the mastoid

0= does not exceed the dorsal margin of the bulla 1= exceeds the dorsal margin of the bulla  
2= mastoid exposed on the cranial roof

Character 19. Shape of the mastoid

0= concave 1= plane 2= convex 3= very inflated

Character 20. Mastoid exposes on the occiput

0= no 1= yes

Character 21. Ventral extension of lateral process of the supraoccipital

0= exceeds the dorsal margin of the bulla 1= extends up to the dorsal margin of the bulla

Character 22. Development of the sinus epitimpanicus

0= small 1= large



Character 23. Size of the postglenoid foramen

0= small 1= large

Character 24. Direction of the paraoccipital process

0= posteroventral 1= anteroventral

Character 25. Tubiform *Meatus Acusticus Externus*

0= absent 1= present

Character 26. Accessory orifice below the *Meatus Acusticus Externus*

0= absent 1= present

Character 27. Posterior extension of the lower incisors

0= up to below the m3 or more 1= up to below the m2 2= up to the m1

Character 28. Height of the condyle

0= high 1= low

Character 29. Development of the mandibular masseteric crest

0= normal 1= reduced

Character 30. Angular process extends more ventrally than the mental keel

0= no 1= yes

Character 31. Discontinuity between the masseteric crest and the fossette for the insertion of the *M. masseter medialis pars infraorbitalis*

0= absent 1= present

Character 32. Location of the insertion for the tendon of the *pars maxilomandibularis*

0= posterior to the level of m1 1= at the level of m1 2= anterior to the level of m1

Character 33. Length of the diastema

0= shorter than the tooth row 1= equal or longer than the tooth row

Character 34. Concavity of the diastema

0= concave 1= plane, diastema almost at the same height of the alveolar line

Character 35. Mental foramen (**non additive**)

0= present, lateral 1= present, dorsolateral 2= absent

Character 36. Cement

0= absent 1= present

Character 37. Hypsodonty

0= braquidont 1= mesodont 2= protohypsodont 3= hypselodont

Character 38. Molarization of the upper premolars (**non additive**)

0= normal replacement, upper premolars without hypocone - hypoflexus

1= normal replacement, upper premolars with hypocone - hypoflexus

2= deciduous premolars retained

Character 39. Penetration degree of the hypoflexus in upper molars (in adults)

0= hypoflexus does not extend more than half way across crowns

1= hypoflexus extends more than half way across crowns

2= hypoflexus crosses completely the crowns

Character 40. Direction of the penetration of the hypoflexus

0= obliquely, opposed to the parafovea 1= transversally, opposed to the protofossa

Character 41. Width of the hypoflexus (**non additive**)

0= normal 1= compressed 2= very thick

Character 42. Third lamina or lobe in M3

0= absent 1= present

Character 43. Asymmetric pattern of the upper and lower teeth

0= absent 1= present

Character 44. Lamination of the dental morphology

0=absent 1= teeth composed by subtriangular lobes 2= teeth composed by rectangular laminae

Character 45. Incisor enamel microstructure

0= multiserial, acute angular 1= multiserial, right angular

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45			
Steirromys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephalomys	1	1	1	1	1	0	1	?	1	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	2	0	1	1	0	1	0	1	1	0	?	1	1	0		
Soriamys	1	0	0	1	2	1	1	0	0	1	1	0	1	0	0	1	0	1	2	0	1	0	0	1	0	1	1	1	0	1	0	2	1	1	1	1	2	0	1	1	2	1	1	1	?			
Lagostomus	2	0	0	0	0	0	1	1	2	1	0	2	2	0	0	0	1	1	1	1	0	1	0	0	2	1	0	0	1	0	?	0	1	0	2	0	3	1	2	0	1	1	0	2	0			
Lagidium	2	?	0	1	1	1	1	0	2	1	0	0	2	0	0	1	1	2	2	1	1	1	2	1	2	1	2	0	1	0	?	2	1	0	1	0	3	1	2	?	1	1	0	2	0			
Chinchilla	2	1	0	1	2	1	1	0	1	1	1	1	1	0	0	1	?	2	3	1	1	1	2	1	2	1	1	0	1	0	?	1	1	0	1	0	3	1	2	?	1	1	0	2	0			
Perimys	1	1	1	1	0	0	1	?	2	1	0	0	2	?	0	0	0	1	0	0	1	0	1	1	1	1	2	0	0	0	0	0	1	0	0	1	3	0	1	0	2	1	0	2	0			
Abrocoma	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	2	3	1	0	0	1	1	0	0	0	0	0	0	1	2	1	0	2	1	3	2	0	1	2	1	1	2	1			
Proechimys	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	2	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	2	0	1	2	0	0	0	0	0	0	1			
Octodontomys	1	1	0	1	1	0	0	0	0	0	0	1	0	2	1	1	1	1	1	2	1	0	0	0	1	0	0	0	0	0	0	1	2	0	0	2	0	3	2	0	?	0	0	0	0	1		

Table 5.— Data matrix of selected characters.

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