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A new chinchilloid (Rodentia, Hystricognathi) from the early Miocene of the localities of Bryn Gwyn and Gran Barranca (Patagonia, Argentina)



Un nouveau chinchilloïde (Rodentia, Hystricognathi) du Miocène inférieur des localités de Bryn Gwyn et Gran Barranca (Patagonie, Argentine)

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ABSTRACT

A new genus and species of chinchilloid rodent is described here. It was found in Colhuehuapian levels (early Miocene) of the localities of Bryn Gwyn and Gran Barranca, Chubut Province, Argentina. The new taxon shows a unique combination of characters (e.g., protohypsodont teeth, upper molars trilophodont, m1 and m2 tri- or tetralophodont with the second crest in position of variable development, and m3 trilophodont, cement absent) that make it different from any other known chinchilloids. We performed a phylogenetic analysis to corroborate the relationships of the new taxon within the Chinchilloidea. Our results indicate that the new taxon is best classified as *Chinchilloidea incertae sedis*, together with *Incamys*, *Garridomys*, and *Scotamys*. These species form the basal stock that leads to the modern lineage Chinchillidae (chinchillas and viscachas). The presence of the new taxon in these localities increases the diversity of chinchilloids during the early Miocene and reduces the dissimilarity between the faunas found in Bryn Gwyn and Gran Barranca.

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R É S U M É

Un nouveau genre et une nouvelle espèce de rongeur chinchilloïde sont ici décrits. Celui-ci a été trouvé dans les niveaux colhuehuapiens (Miocène inférieur des localités de Bryn Gwyn et de Gran Barranca, province de Chubut, Argentine). Le nouveau taxon montre une combinaison unique de caractères (à savoir, dents protohypsodontes, molaires supérieures trilophodontes, m1 et m2 tri- ou tétralophodontes avec la seconde crête en position de développement variable et m3 trilophodonte, ciment absent) qui le rend différent de tous les autres chinchilloïdes connus. Une analyse phylogénétique a été réalisée pour confirmer les relations du nouveau taxon au sein des Chinchilloidea. Nos résultats montrent que le

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nouveau taxon se classe au mieux en tant que Chinchilloidea *incertae sedis*, avec *Incamys*, *Garridomys* et *Scotamys*. Ces espèces forment le stock basal qui conduit à la lignée moderne des Chinchillidae (chinchillas et viscachas). La présence du nouveau taxon dans ces localités augmente la diversité des chinchilloïdes pendant le Miocène inférieur et réduit la différence entre les faunes trouvées à Bryn Gwyn et à Gran Barranca.

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1. Introduction

Chinchilloidea is a very distinguished group within the South American hystricognath rodents (Caviomorpha) and is currently represented by pacaranas, chinchillas, and vizcachas, comprising four genera (*Dinomys* Peters, 1873; *Chinchilla* Bennet, 1829; *Lagidium* Meyen, 1833; and *Lagostomus* Brookes, 1828) and eight species (Spotorno and Patton, 2015). However, the fossil record shows a large number of extinct forms known from the Oligocene onwards, and its acme is inferred during the late Miocene with at least twenty genera, indicating that chinchilloids were much more diverse in the past (Vucetich et al., 2015a). The monophyly of Chinchilloidea has been corroborated in phylogenetic analyses based on molecular (e.g., Blanda-Kanfi et al., 2009; Fabre et al., 2012, 2013; Huchon and Douzery, 2001; Upham and Patterson, 2015) and morphological data (e.g., Arnal and Vucetich, 2015; Kerber and Sánchez-Villagra, 2018; Kerber et al., 2017a, 2017b, 2018; Rasia and Candela, 2018a, 2018b).

Chinchilloidea are undoubtedly known since the early Oligocene (Tinguirirican–pre Deseadan faunas) in Chile (Bertrand et al., 2012; Flynn et al., 2003) and Argentina (Vucetich et al., 2010a), and since then their fossil record is relatively continuous and broadly distributed in the continent. During the Deseadan, South American Land Mammals Age (SALMA) they were already moderately diverse, with representatives from Patagonia and Bolivia (Busker and Dozo, 2017; Hoffstetter and Lavocat, 1970; Loomis, 1914; Patterson and Wood, 1982; Pérez et al., 2018; Vucetich, 1989; Vucetich et al., 2015b). The dental morphology of the extant Chinchilloidea is characterized by high-crowned teeth without root formation (euhypsodont condition) and laminated cheek-teeth, whereas the fossil forms show a larger dental morphological diversity (Kramarz et al., 2013, 2015; Rasia, 2016; Rasia and Candela, 2018a, 2018b; Vucetich et al., 2015a). The presence of hypsodonty in *Eoviscaccia frasinetti* Bertrand et al., 2012 during the early Oligocene indicates that the superfamily acquired this condition earlier than the other caviomorphs in their evolutionary history (Bertrand et al., 2012; Vucetich, 1989; Vucetich et al., 2015a). Several genera retain a more generalized dental morphology until the Colhuehuapian SALMA (early Miocene; Flynn and Swisher, 1995) (Kramarz et al., 2013; Vucetich et al., 2015a). The chinchilloid diversity during the Colhuehuapian is relatively poor and only *Perimys* Ameghino, 1887, *Garridomys* Kramarz et al., 2013 and *Eoviscaccia australis* Vucetich, 1989 are known (Kramarz, 2001a; Kramarz, 2002; Kramarz et al., 2013; Rasia, 2016; Vucetich, 1989; Vucetich et al., 2010b, 2015a). After the

Colhuehuapian SALMA, the specific diversity increased and the late Miocene is the acme of chinchilloids represented by a great taxonomical diversity (e.g., eumegamylines) and some very large size representatives (e.g., *Phoberomys* Kraglievich, 1926; *Josephoartigasia* Mones, 2007; *Neoeptiblenia* Ameghino, 1889) (Horovitz et al., 2006; Kerber et al., 2017a, 2017b, 2018; Rasia and Candela, 2018a, 2018b; Rinderknecht and Blanco, 2008; Vucetich et al., 2015a).

The best known Colhuehuapian SALMA localities in Patagonia, Gran Barranca and Bryn Gwyn (Chubut Province, Argentina) have the highest record and diversity of caviomorph rodents (Vucetich et al., 2010b). Bryn Gwyn is 8 km apart from the locality of Gaiman (eastern Chubut Province), in the Lower Valley of the Chubut River (Fig. 1; Simpson, 1940), whilst Gran Barranca is placed near Lake Colhue Huapi (southeastern Chubut Province, Madden et al., 2010) (Fig. 1). These localities have been prospected for more than one century, but only two taxa of chinchilloids were described, *Eoviscaccia australis* and *Perimys* (several species) (Vucetich et al., 2010b). In this contribution, we describe a new genus and species of chinchilloid rodent from the early Miocene of the localities of Bryn Gwyn and Gran Barranca. A cladistic analysis was performed in order to test the phylogenetic relationships of the new species within Chinchilloidea.

2. Materials and methods

The new genus and species is represented by several isolated teeth and five well-preserved mandibular fragments. These materials were collected during several field trips in 1990 and 1992 by members of the Laboratory of Paleontology of the Centro Nacional Patagónico (CENPAT, Puerto Madryn, Chubut) and the Museo de La Plata (MLP, La Plata, Buenos Aires), and during trips from 2007 to 2018 by members of the Museo Paleontológico Egidio Feruglio (MEF, Trelew, Chubut). The specimens are housed at the Museo Paleontológico Egidio Feruglio.

2.1. Institutional abbreviations

MPEF-PV, Museo Paleontológico Egidio Feruglio, Paleontología de Vertebrados, Trelew, Chubut, Argentina.

2.2. Dental and mandibular nomenclature

For dental nomenclature, we followed Arnal and Vucetich (2015) (Fig. 2A and B), and for mandibular nomenclature we followed a modified version of Pérez (2010) (Fig. 2C).

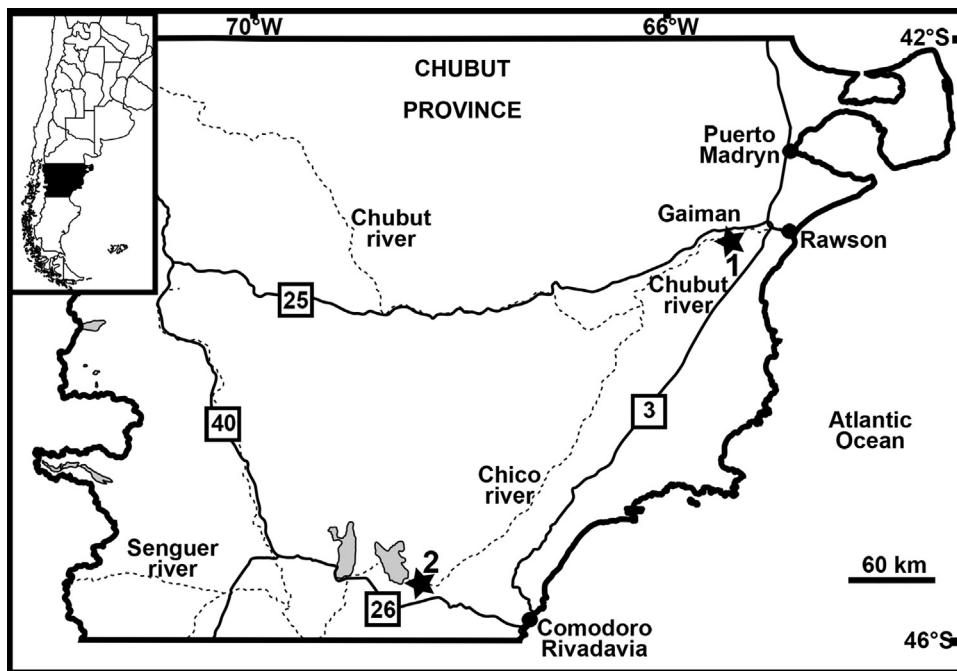


Fig. 1. Location map with localities where *Saremmys ligcura* is registered. The stars indicate the localities: 1. Bryn Gwyn; 2. Gran Barranca, Chubut Province, Argentina.

Fig. 1. Carte de localisation des sites dans lesquels *Saremmys ligcura* a été enregistré. Les étoiles indiquent les sites : 1. Bryn Gwyn; 2. Gran Barranca, province de Chubut, Argentine.

2.3. Dental nomenclature abbreviations

Upper tooth: **A**, anteroloph; **H**, hypocone; **Hf**, hypoflexus; **M**, metacone; **Msf**, mesoflexus/mesofossette; **Mt**, metaloph; **Mtf**, metaflexus/metafossette; **P**, protocone; **Pa**, paracone; **Pf**, paraflexus/parafossette; **Pr**, protoloph; **Ps**, posteroloph.

Lower tooth: **Af**, anteroflexid/anterofossettoid; **E**, entoconid; **Hd**, hypoconid; **Hfi**, hypoflexid; **Hpl**, hypolophid; **Med I**, metalophulid I; **Met**, metaconid; **Msi**, mesostilid; **Msf**, mesoflexid/mesofossettoid; **Mtf**, metaflexid/metafossettoid; **Prt**, protoconid; **Pst**, posterolophid.

2.4. Mandibular nomenclature abbreviations

Mandibular nomenclature: **C**, condyle; **Ch**, chin; **Cp**, coronoid process; **Hc**, horizontal crest; **Mas**, masseteric fossa; **Masd**, dorsal masseteric fossa; **Mc**, masseteric crest; **Mf**, mental foramen; **N**, notch for the insertion of the muscle *masseter medialis pars infraorbitalis*.

2.5. Phylogenetic analysis

In order to test the phylogenetic position of the new species and the relationships within Chinchilloidea, a cladistic analysis was performed based on the data matrix of [Rasia and Candela \(2018a\)](#). This matrix is a modification of previous versions (e.g., [Kramarz et al., 2013](#)). We have modified it by including three more taxa (*Incarnys*

bolivianus [Hoffstetter and Lavocat, 1970](#); *Scotamys antiquus* [Loomis, 1914](#); and *Saremmys ligcura*), modifying four characters (2, 21, 42, and 43) and adding five new characters (46–50) ([Appendix A](#)). We used Mesquite 3.11 ([Maddison and Maddison, 2011](#)) for editing the data matrix. The new dataset resulted in 20 taxa and 50 morphological characters, of which seven characters were considered ordered ([Appendix B](#)). Heuristic parsimony analysis was performed in TNT version 1.5 ([Goloboff and Catalano, 2016](#); [Goloboff et al., 2008](#)), using 1000 replications of Wagner trees using random addition sequences followed by a Tree Bisection Reconnection (TBR) branch swapping algorithm (holding ten trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Equally weighted parsimony was used to minimize the number of postulated evolutionary transformations. The most parsimonious trees (MPTs) were summarized in a strict consensus, and support was calculated with absolute Bremer support ([Bremer, 1994](#); [Goloboff and Farris, 2001](#)).

3. Results

3.1. Systematic Paleontology

Rodentia [Bowdich, 1821](#)
 Hystriognathi [Tullberg, 1899](#)
 Caviomorpha Wood & Patterson in [Wood, 1955](#)
 Pan-Chinchilloidea [Kraglievich, 1940](#) (sensu [Bertrand et al., 2012](#))

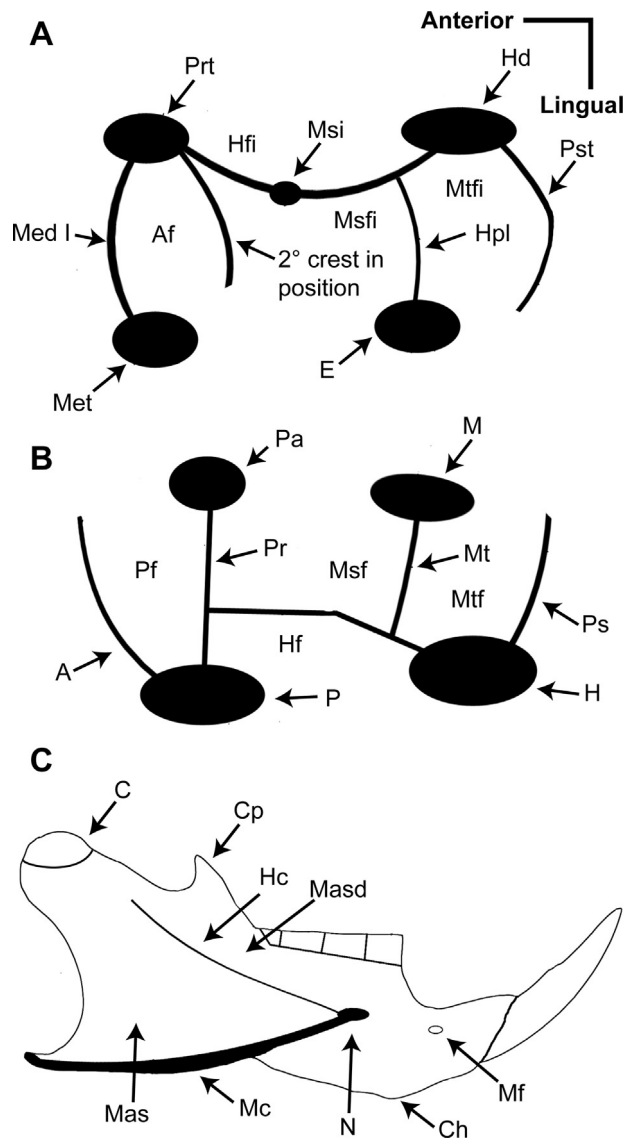


Fig. 2. Dental nomenclature modified from Arnal and Vucetich (2015) and mandibular nomenclature, modified from Pérez (2010). A hypothetical mandible was made in order to show all the mentioned structures. A. Lower tooth abbreviations: **2° cr**, second crest in position; **af**, anteroflexid/anterofossettoid; **e**, entoconid; **h**, hypoconid; **hld**, hypolophid; **m**, metaconid; **med I**, metalophulid I; **msf**, mesoflexid/mesofossettoid; **mt**, metaflexid/metafossettoid; **p**, protoconid; **pam**, posterior arm of the metaconid; **psd**, posterolophid. B. Upper tooth abbreviations: **Al**, anteroloph; **hf**, hypoflexus; **ms**, mesolophule; **Msf**, mesoflexus/mesofossette; **Mt**, metaflexus/metafossette; **Mel**, metaloph; **Pf**, paraflexus/parafosette; **Prl**, protoloph; **PsI**, posteroloph. C. **C**, condyle; **Ch**, chin; **Cp**, coronoid process; **Hc**, horizontal crest; **Mas**, masseteric fossa; **Masd**, dorsal masseteric fossa; **Mc**, masseteric crest; **Mf**, mental foramen; **N**, notch for the insertion of the muscle *masseter medialis pars infraorbitalis*.

Fig. 2. Nomenclature dentaire modifiée d'après Arnal et Vucetich (2015) et nomenclature mandibulaire modifiée d'après Pérez (2010). Une mandibule hypothétique a été réalisée de manière à montrer toutes les structures mentionnées. A. Abréviations relatives aux dents inférieures : **2° cr**, seconde crête en position ; **af**, antéroconide/antérofossettide ; **e**, entoconide ; **h**, hypoconide ; **hld**, hypolophide ; **m**, métaconide ; **med I**, métalophulide ; **msf**, mésolflexide/mésosfossettide ; **mt**, métaflexide/métafossettide ; **p**, protoconide ; **pam**, branche postérieure du métaconide ; **psd**, postérolophide. B. Abréviations relatives aux dents supérieures : **Al**, antéroloph ; **hf**, hypoflexus ; **ms**, mésolophule ; **Msf**, mésolflexus/mésosfossette ; **Mt**, métaflexus/métafossette ; **Mel**, métalophe ; **Pf**, paraflexus/parafosette ; **Prl**, protolophe ; **PsI**, postéroloph. C. **C**, condyle ; **Ch**, chin ; **Cp**, processus coronoïde ; **Hc**, crête horizontale ; **Mas**, fosse du masséter ; **Masd**, fosse dorsale du masséter ; **Mc**, crête du masséter ; **Mf**, foramen mental ; **N**, encoche pour l'insertion du muscle *masseter medialis pars infraorbitalis*.

Saremmys gen. nov.

Derivation of name. In honor to SAREM (Sociedad Argentina para el Estudio de los Mamíferos) for the invaluable contributions to the knowledge and conservation of the Argentinian mammal fauna, as well as educational and

outreach activities encouraged by this society for more than thirty years.

Type and only species. *Saremmys ligcura* sp. nov.

Distribution. Bryn Gwyn locality, southern cliff of the Chubut River, Trelew Member (friable level) and Gran Barranca locality, in levels of the Sarmiento Formation in both

localities, Chubut Province (Fig. 1), Colhuehuapian SALMA (early Miocene) (Flynn and Swisher, 1995; Simpson, 1940; Vucetich et al., 2010b).

Diagnosis. As for the type and only species of the genus. *Saremmys ligcura* sp. nov. (Figs. 3–9)

Derivation of name. From the mapuzungun (mapuche dialect) lig, white, and cura, stone, due to the predominant white color of the outcrops in both Bryn Gwyn and Gran Barranca.

Holotype. MPEF-PV 11340, left mandibular fragment with incisor, p4–m3.

Diagnosis. Caviomorph larger than *Garridomys*, but smaller than *Scleromys*; protohypsodont, differing from *Australoprocta*, which is mesodont; upper molars trilophodont, differing from *Garridomys* and *Incamys*, which are tetralophodont and *Australoprocta*, that is, pentalophodont; m1 and m2 tri- or tetralophodonts with the second crest in position of variable development, differing from *Incamys* and *Australoprocta*, which are always tetralophodont, and from *Garridomys*, which does not have the second crest in position complete in the lower molars; m3 trilophodont, differing from *Australoprocta*, which is tetralophodont; two or three fossettids and two fossettes persistent, different than in *Garridomys*, which always has two fossettes or fossettids; hypoflexus/hypoflexid joined to paraflexus/metaflexid in juvenile and adult stages; enamel band complete and uniform, different than in *Garridomys*; cement absent, different from *Scleromys* and *Garridomys*; dp4 pentalophodont; p4 with mesostylid as in *Garridomys* and *Scleromys*; anterior notch present on p4 in juvenile stages in contrast to *Garridomys*; metalophulid I on p4 appears with wear; posteroventral projection of the posterior end of the mandibular symphysis (chin) anterior to p4, different than in *Scleromys*, *Incamys* and *Garridomys* in which it is posterior to p4; anterior border of the notch for the *mmpi* muscle below to m1, differing from *Garridomys* and *Incamys*, in which it is anterior; the root of the incisor shorter than in *Garridomys* and *Incamys*; mental foramen dorsolaterally located, differing from *Scleromys* and *Garridomys*, in which is more laterally located.

Referred material. MPEF-PV 11341, right mandibular fragment with p4–m3; MPEF-PV 11342, left mandibular fragment with m1–m3; MPEF-PV 11343, left mandibular fragment with m1–m2; MPEF-PV 11344, right mandibular fragment with m2; MPEF-PV 11345, right p4; MPEF-PV 11346a, left dp4; MPEF-PV 11346b right p4; MPEF-PV 11347a, right m1 or m2; MPEF-PV 11347b, left m1; MPEF-PV 11347c, left m1 or m2; MPEF-PV 11347d, left m1 or m2; MPEF-PV 11348a, right M1 or M2; MPEF-PV 11348b, right dp4; MPEF-PV 11348c, right dp4; MPEF-PV 11348d, left dp4; MPEF-PV 11349a, right dp4; MPEF-PV 11349b, isolated M1 or 2; MPEF-PV 11349c, isolated left M3; MPEF-PV 11349d, isolated left p4; MPEF-PV 11349e isolated left p4; MPEF-PV 5058, right m1 or m2; MPEF-PV 5036a, left p4, right p4, isolated left m1; MPEF-PV 5036b, isolated left m2; MPEF-PV 5036c, isolated left M1 or M2; MPEF-PV 5004, right mandibular fragment with m1–m3; MPEF-PV 5421, isolated left M1 or M2.

Geographic and stratigraphic occurrence. The holotype and all but one of the referred specimens come from a deposit of friable tuff above the nodular calcrete located in the base of the Trelew Member in La Cantera (see Bown and Fleagle, 1993; Kay et al., 2008; Kramarz, 1998) and El Camino (S 43°21'41.10" W 65°27'56.1") sites of the Sarmiento Formation, Bryn Gwyn, southern margin of the Lower Valley of the Chubut River, Chubut Province (Fig. 1). Only MPEF-PV 5421 comes from Gran Barranca locality, Chubut Province (Fig. 1), Colhuehuapian SALMA (early Miocene, Kay et al., 2008; Scasso and Bellosi, 2004; Vucetich et al., 2010b).

3.1.1. Description

Mandible. The mandible (Fig. 3) is slightly smaller and more slender than that of *Scleromys Ameghino, 1887* and *Garridomys* (Kramarz et al., 2013). The diastema is similar to the condition of *Scleromys* and slightly more concave and shorter than in *Perimys*, *Prolagostomus Ameghino, 1887* and the extant forms (e.g., *Lagidium*, *Lagostomus*). The mental foramen is present as in the other chinchilloids and is dorsolabially located as in *Incamys* (Fig. 3A), but unlike *Garridomys* and *Scleromys*, in which the foramen is more laterally located.

In labial view (Fig. 3A–C), the posteroventral projection of the posterior end of the mandibular symphysis (chin) is prominent, similar to the condition of *Scleromys*. It is located at the anterior level of the premolar (Fig. 3A) as in the extant genera and differs from *Incamys* and *Scleromys*, in which the chin is at level of p4, and from *Garridomys*, in which it is posterior to the p4. The notch for the insertion of the muscle masseter medialis pars infraorbitalis (*mmpi*) is placed at the level of the m1 (Fig. 3A and J), differing from *Garridomys* and *Incamys*, in which the *mmpi* is anterior to the m1. The *mmpi* is slightly developed as in other chinchillids and joined to the masseteric crest. The lateral crest is straight, the horizontal crest is reduced, and the dorsal portion of the masseteric fossa (i.e. fossa for the masseter medialis pars posterior muscle, *sensu* Rasia and Candela [2018a–c.39]) is extended posterior to the m3 up to the anterior portion of the condyle (Fig. 3A and G). The masseteric crest is developed as in *Scleromys*, *Incamys*, and *Garridomys*, but contrasts with the condition of the extant forms. The coronoid process arises at the posterior level of the m3, but is dorsally broken in all the specimens (Fig. 3A, D and G). The condyle is rounded, antero-posteriorly short and slightly above the level of the tooth row (Fig. 3A), contrasting with the condition of the extant chinchillids, in which the condyle is much higher than the tooth row.

On the lingual side, the hystricognathus groove is deep, the retromolar fossa is shallow, and the mandibular foramen is placed behind it and below the level of the molars (Figs. 3B, H and K). Such a condition differs from the extant forms, in which the mandibular foramen is within the retromolar fossa.

Teeth. The teeth of *Saremmys* are larger than those of *Garridomys*, but smaller than those of *Scleromys* (Tables 1 and 2). The molariforms are protohypsodont (*sensu* Mones, 1982) (Fig. 4), similar to those of *Garridomys*, *Incamys*, and *Scleromys*, but different from *Australoprocta*, Kramarz, 1998; in which the teeth are mesodont. Cement is

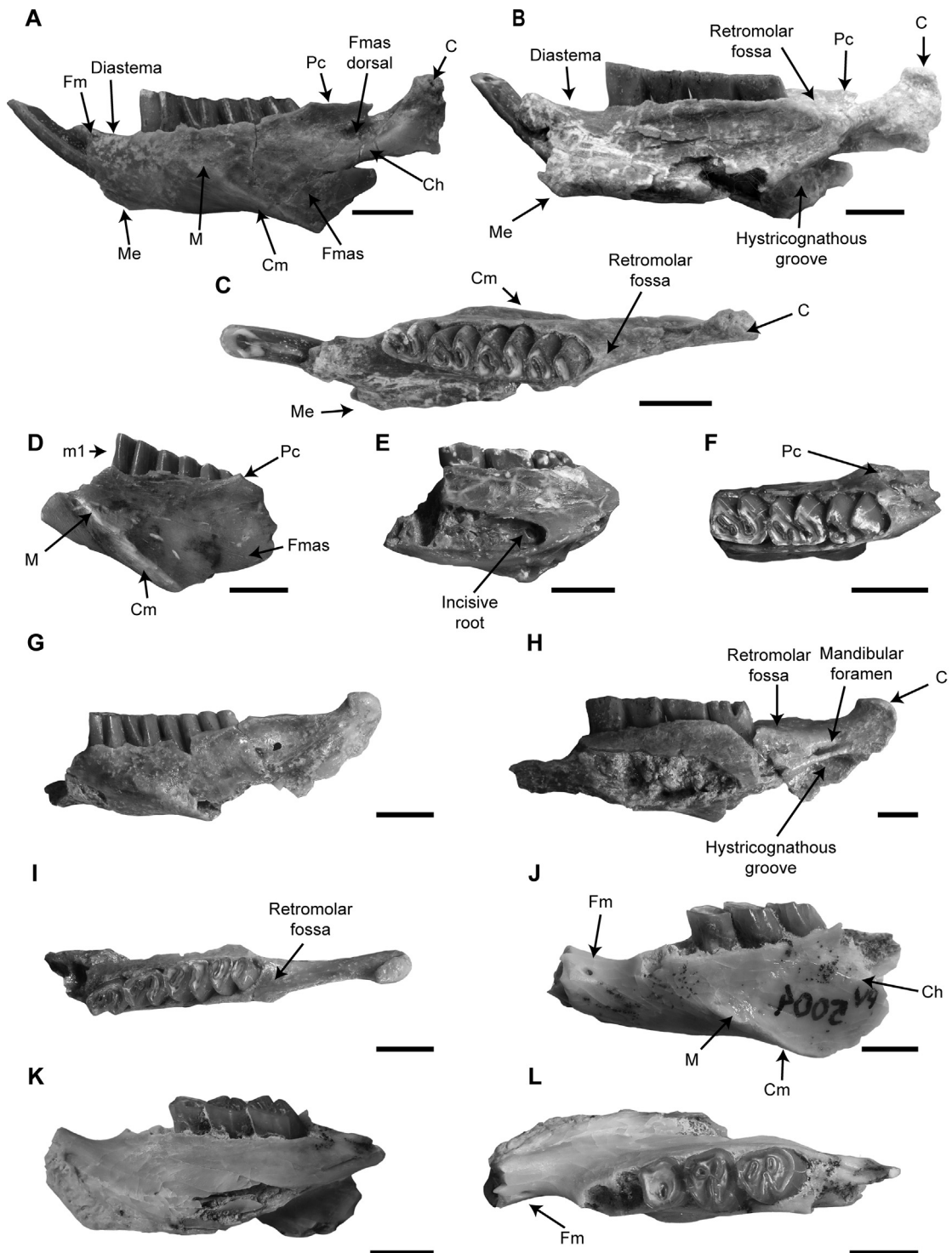


Fig. 3. Lateral, medial and occlusal views of the mandible of *Saremmys ligcura*. A and B (reversed), C (reversed) MPEF-PV 11340 (holotype); D and E (reversed) F (reversed) MPEF-PV 11342; G (reversed), H, I MPEF-PV 11341; J (reversed), K and L MPEF-PV 5004. All scales are 5 mm. Anterior to the left.

Fig. 3. Vues latérale, médiale et occlusale de la mandibule de *Saremmys ligcura*. A et B (retournées), C (retournée) MPEF-PV 11340 (holotype) ; D et E (retournées), F (retournée) MPEF-PV 11342 ; G (retournée), H, I MPEF-PV 11341 ; J (retournée) ; K et L MPEF-PV 5004. Toutes les barres d'échelle représentent 5 mm. Avant vers la gauche.

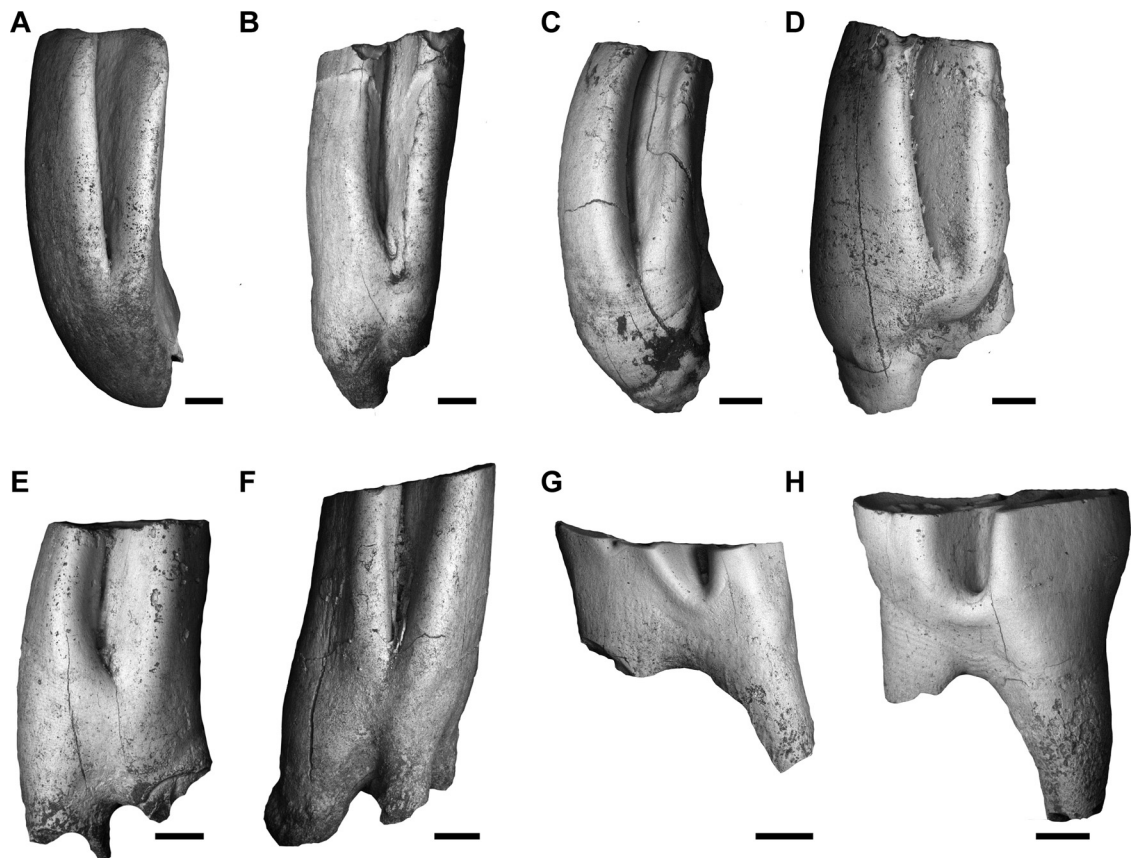


Fig. 4. Labial view of the tooth of *Saremmys ligcura*. A. MPEF-PV 11349b. B. MPEF-PV 11347c. C. MPEF-PV 5021. D. MPEF-PV 11345 (reversed). E. MPEF-PV 5036a. F. MPEF-PV 5058. G. MPEF-PV 11346a (reversed). H. MPEF-PV 11349a (reversed). All scales are 1 mm. Anterior to the left.

Fig. 4. Vue labiale d'une dent de *Saremmys ligcura*. A. MPEF-PV 11349b. B. MPEF-PV 11347c. C. MPEF-PV 5021. D. MPEF-PV 11345 (retournée). E. MPEF-PV 5036a. F. MPEF-PV 5058. G. MPEF-PV 11346a (retournée). H. MPEF-PV 11349a (retournée). Toutes les barres d'échelle représentent 1 mm. Avant vers la gauche.

absent as in *Incamys* and *Australoprocta*. The enamel is complete and uniformly distributed (Fig. 5) as in *Australoprocta*, while in *Garridomys* and *Incamys menniorum* Vucetich et al., 2015b the enamel is not uniform (Kramarz et al., 2013; Patterson and Wood, 1982; Vucetich et al., 2015b).

Incisors. The lower incisor is well preserved in the holotype (MPEF-PV 11340). It is robust as in *Scleromys*, with the anterior wall plane and not laterally compressed (*sensu* Arnal and Vucetich, 2015). It is extended to the m3, differing from *Garridomys* and *Incamys*, in which the incisor is longer, extending beneath m3.

dp4. The dp4 has two roots (Fig. 4H) and is antero-posteriorly elongated and pentalophodont (Fig. 6A). The protoconid is aligned with the hypoconid. The metalophulid I is short and slightly curved, lingually joined to a conspicuous metaconid (Fig. 6A). Posteriorly to the metaconid is a cusp with a labial projection that we interpret as mesostylid with a short crest (neomesolophid? *sensu* Boivin et al., 2017). The mesolophid is straight, short and is in contact with a long ectolophid. The hypolophid is straight and wider than the other lophids. The posterolophid is long and strongly oblique, and separated by the metaflexid plus hypoflexid from the hypolophid.

Antero-lingually to the posterolophid is a small cusp that could be an intraspecific variation.

With little more wear (Fig. 6B), the occlusal morphology is simplified and forms a large anterofossettid, which in some specimens is divided into two smaller ones (Fig. 6C). The mesoflexid is oblique and still open. The hypoflexid is also strongly oblique and fused to the metaflexid. In MPEF-PV 11348C (Fig. 6D), there is a small labial flexid, anterior to the hypoflexid. We interpret this flexid as an individual variation. When the dp4 is worn (Fig. 6D and E), the lingual wall becomes straight, whilst the anterior and posterior ones become rounded. The fossettids are small and shallow, and the hypoflexid is still open.

p4. The trigonid is labio-lingually narrower than the talonid (Fig. 7), as in *Incamys*, *Australoprocta*, and *Garridomys*. In unworn specimens (Fig. 7A–C), the cusps are developed and quite bulky. The protoconid is labiolingually aligned with the metaconid, which is conspicuous. Posteriorly to the metaconid is a noticeable mesostylid, as in the juvenile specimens of *Scleromys* and *Garridomys*. The metalophulid I is not visible in juvenile stages, because of a deep anterior notch between the proto- and metaconid, different than in *Incamys*. In *Saremmys*, with wear, the notch is

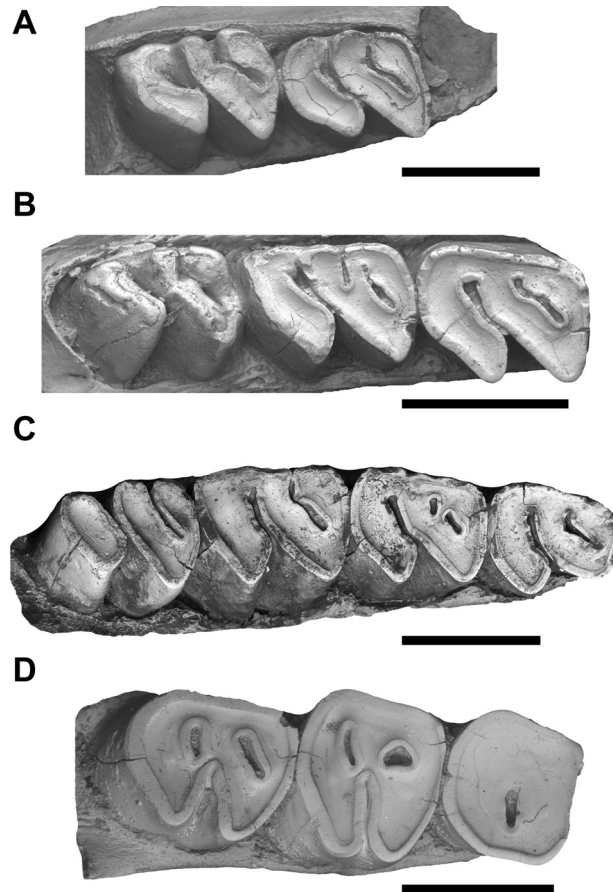


Fig. 5. Occlusal view of the tooth rows of *Saremmys ligcura*. A. MPEF-PV 11343 (reversed). B. MPEF-PV 11342 (reversed). C. MPEF-PV 11341. D. MPEF-PV 5004. All scales are 4 mm. Anterior to the right.

Fig. 5. Vue occlusale d'une barre de dents de *Saremmys ligcura*. A. MPEF-PV 11343 (retournée). B. MPEF-PV 11342 (retournée). C. MPEF-PV 11341. D. MPEF-PV 5004. Toutes les barres d'échelle représentent 4 mm. Avant vers la droite.

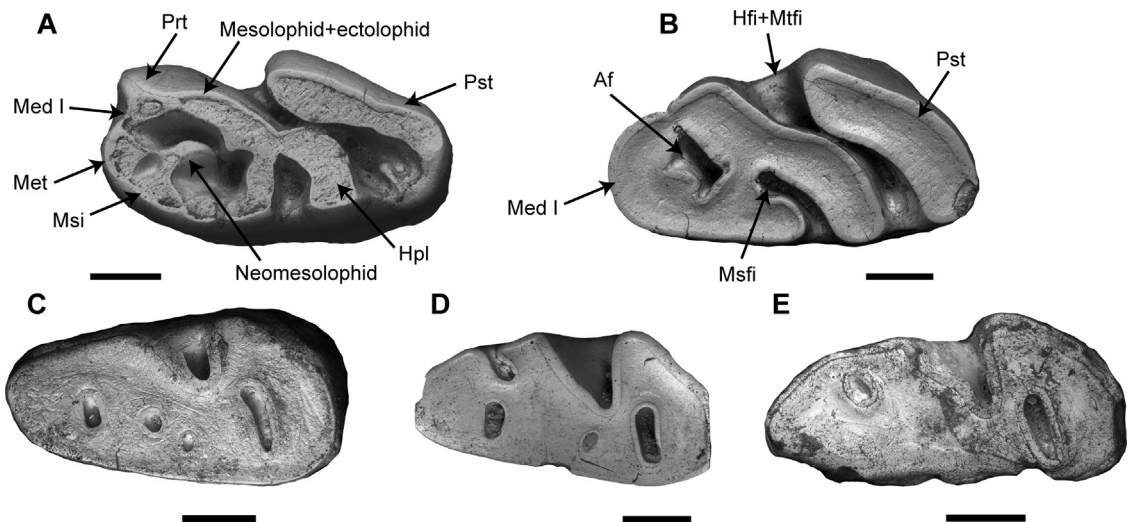


Fig. 6. dp4 of *Saremmys ligcura*. A. MPEF-PV 11348b. B. MPEF-PV 11349a. C. MPEF-PV 11348d (reversed). D. MPEF-PV 11346a (reversed). E. MPEF-PV 11348c. All scales are 1 mm. Anterior to the left.

Fig. 6. dp4 de *Saremmys ligcura*. A. MPEF-PV 11348b. B. MPEF-PV 11349a. C. MPEF-PV 11348d (retournée). D. MPEF-PV 11346a (retournée). E. MPEF-PV 11348c. Toutes les barres d'échelle représentent 1 mm. Avant vers la gauche.

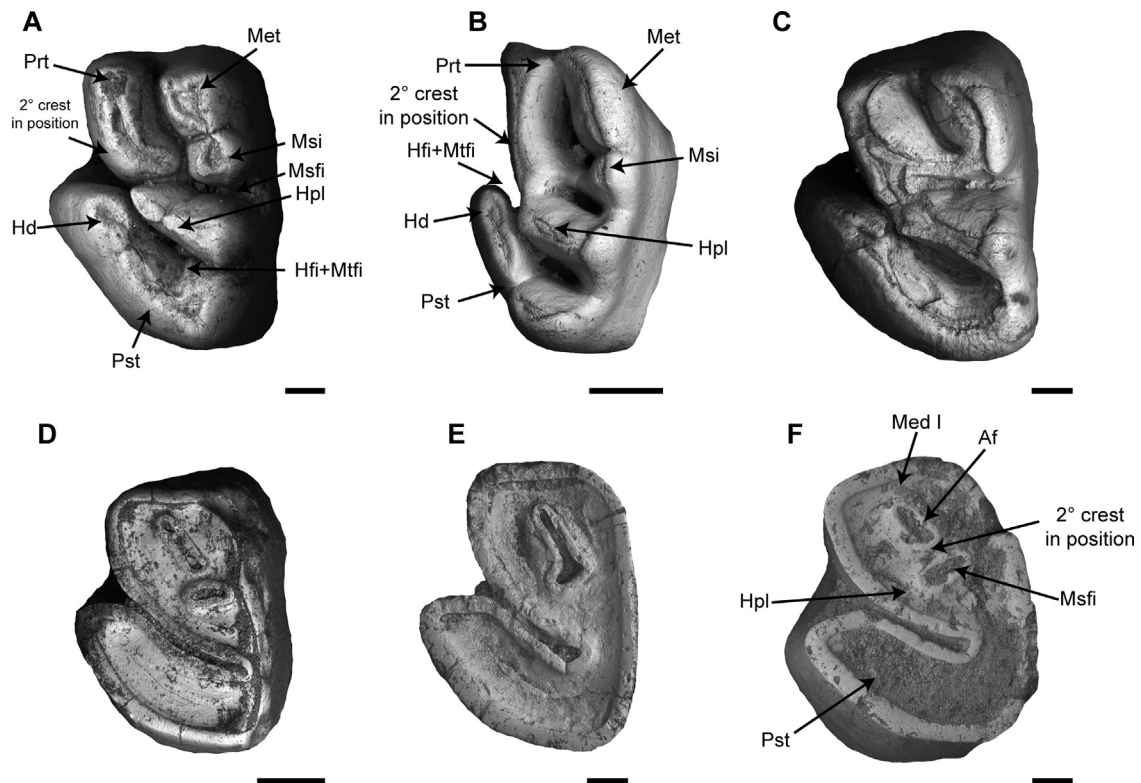


Fig. 7. p4 of *Saremmys ligcura*. A. MPEF-PV 11349E. B. MPEF-PV 11346B (reversed). C. MPEF-PV 11349d. D. MPEF-PV 11345 (reversed). E. MPEF-PV 5036a (reversed). F. MPEF-PV 5036a. All scales are 500 μ m, except B and D, 1 mm.

Fig. 7. P4 de *Saremmys ligcura*. A. MPEF-PV 11349E. B. MPEF-PV 11346B (retournée). C. MPEF-PV 11349d. D. MPEF-PV 11345 (retournée). E. MPEF-PV 5036a (retournée). F. MPEF-PV 5036a. Toutes les barres d'échelle représentent 500 μ m, sauf B et D représentant 1 mm.

lost and the metalophulid I reaches the occlusal surface. This sequence is also seen in *Garridomys* and *Scleromys*. The second crest in position emerges from the protoconid and it has a variable development. In some specimens, this crest is short and curved (Fig. 7A), and in others it is long and joined to the mesostylid (Fig. 7B). The hypolophid is almost straight and labially oriented, and is isolated from the other crests. The posterolophid extends from the hypoconid and is oblique. The mesoflexid is labiolingually open and the hypoflexid is joined to the metaflexid (taeniodont pattern).

With more wear (Fig. 7D–F), the metalophulid I is well developed. When the second crest in position is short, the antero- and mesofossettid are fused and form a unique fossettid; when it is long, the antero- and mesofossettid are isolated (Fig. 7C and E). The hypolophid is joined to a short ectolophid. The posterolophid is antero-posteriorly enlarged, acquiring a laminar shape. The hypoflexid plus metaflexid is lingually closed, forming a long flexid that remains open. The p4 forms two well-developed roots, anteroposteriorly aligned (Fig. 4G and H).

Lower molars. The occlusal pattern of the lower molars is tri- or tetralophodont, with the second crest in position variably developed (Fig. 8) similar to the condition of *Scleromys*. The general wear pattern of the occlusal surface is similar to that of p4. The specimen MPEF-PV 11347b (Fig. 8A) is relatively juvenile and the metalophulid I is long and straight. The second crest in position is partially

developed towards the labial side. The mesoflexid and the meta- plus hypoflexid are still open. The hypolophid is long and oblique. The posterolophid is long, wide and curved, and it is isolated from the other crests. The m3 is always trilophodont and has a shorter posterolophid than m1 and m2 (Fig. 5). With more wear, the lingual flexids become closed, the anterior and lingual walls of the molars are straight, and the posterior wall is curved (Fig. 8B–D). The trigonid acquires a triangular outline, while the talonid (only formed by the posterolophid) is laminar (Fig. 8E). In more advanced stages of wear, the contour of the teeth become more rounded with the curved anterior and posterior walls (Fig. 8F). The meta- and hypoflexid are divided, and only two small fossettids remain (antero- and metafossettid). The hypoflexid is labiolingually shorter and forms a small hypofossettid in very late ontogenetic stages (Fig. 5D).

Upper molars. The occlusal pattern is trilophodont, (Fig. 9), contrasting with the condition of *Incarnys* and *Garridomys* (Kramarz et al., 2013). The hypocone is more labial than the protocone and the anteroloph is long, curved and laminar-shaped (Fig. 9A). It is separated from the protoloph by the hypoflexus plus paraflexus during the first stages of wear (Fig. 9A). The hypoflexus is funnel-like, wider in its lingual portion, as already stated by Kramarz et al. (2013). The antero-labial corner of the anteroloph is enlarged. The protoloph is long, curved and reaches

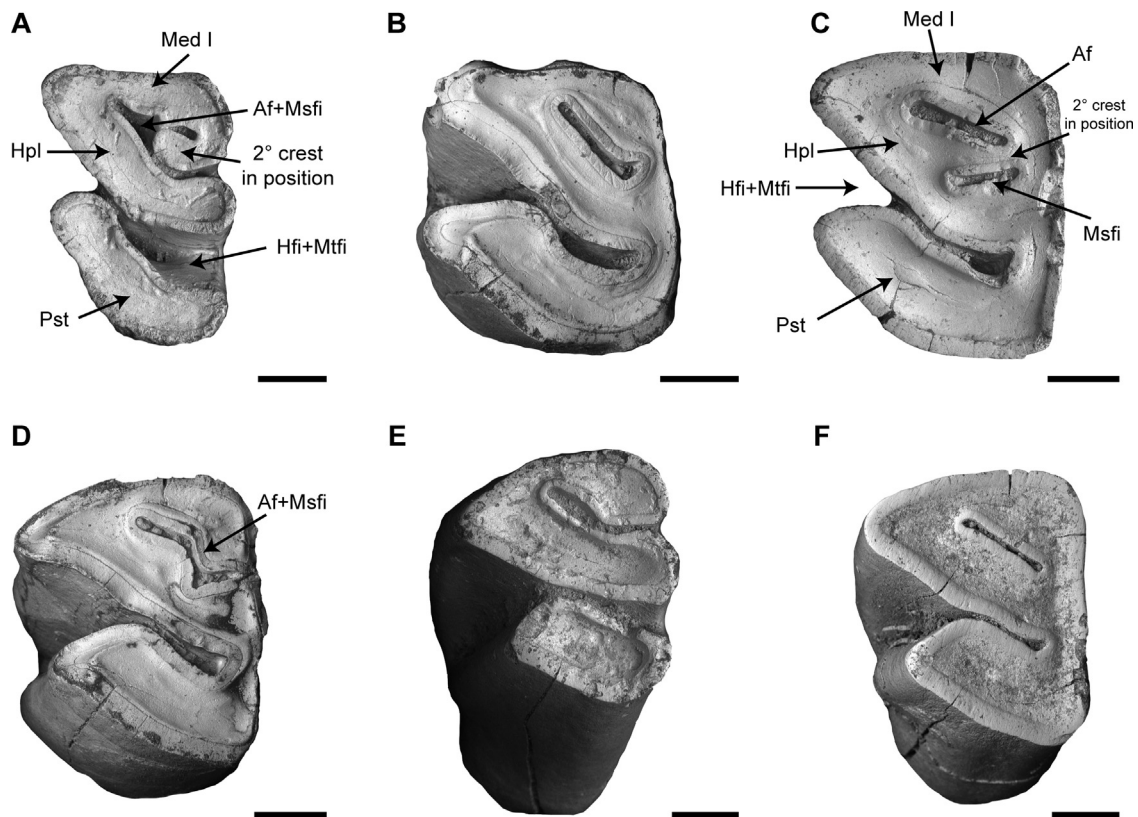


Fig. 8. Lower molars of *Saremmys ligcura*. A. MPEF-PV 11347B. B. MPEF-PV 11347D. C. MPEF-PV 11347A. D. MPEF-PV 11347C. E. MPEF-PV 5036A. F. MPEF-PV 5058. All scales are 1 mm.

Fig. 8. Molaires inférieures de *Saremmys ligcura*. A. MPEF-PV 11347B. B. MPEF-PV 11347D. C. MPEF-PV 11347A. D. MPEF-PV 11347C. E. MPEF-PV 5036A. F. MPEF-PV 5058. Toutes les barres d'échelle représentent 1 mm.

the hypocone postero-lingually (Fig. 9A and B). The posteroloph is shorter than the other crests and is posteriorly convex (Fig. 9A and B). The metaflexid is oblique, long and wide, and becomes closed first (Fig. 9C and D). In more advanced stages of wear, the parafofsette is formed and the hypoflexid is shorter (Fig. 9C). The anterior lobe (only formed by anteroloph) acquires a rectangular shape and the posterior one is triangular in outline (Fig. 9C). The M3 (Fig. 9D) has a more triangular posterior lobe, clearly narrower than the M1–M2, and a more curved protoloph. Also, the M3 is smaller than the other molars.

The specimen MPEF-PV 5421 from Gran Barranca was briefly described by Vucetich et al. (2010b) and assigned to Chinchilloidea indet. Then, Kramarz et al. (2013) also briefly described the molar. Despite being similar to *Garridomys*, the authors point out several differences with the materials assigned to this species and also assigned it as a Chinchilloidea indet. Here, we assign MPEF-PV 5421 to *S. ligcura* because the tooth is trilophodont, with homogeneous enamel band, without cement, protohypodont and hypoflexus join paraflexus.

Remarks. *Australoprocta* (Kramarz, 1998) was found in Bryn Gwyn (Trelew Member, early Miocene) and assigned to Dasyproctidae (Cavoidea). Despite some similarities, it differs from *Saremmys* in several striking characters, such as a lower crown tooth and tetralophodont upper

molars (see above). However, the phylogenetic position of *Australoprocta* has never been tested. The revision of *Australoprocta* and its phylogenetic relationships is being performed by one of the authors (MEP).

3.2. Phylogenetic analysis

The parsimony cladistic analysis of the morphological matrix resulted in eight MPTs of 128 steps. The strict consensus of all MPTs is shown in Fig. 10. The consensus coincides with the results of Rasia and Candela (2018a) in retrieving the monophyly of Dinomyidae, Chinchillidae and Neopiblemyidae (see unambiguous synapomorphies in Appendix C).

The phylogenetic analysis places *Saremmys ligcura* (Fig. 10, Node C) among the most basal forms of Chinchillidae + Neopiblemyidae (Fig. 10, Node E). The new taxon clusters with *Scotamys*, and the clade of *Eoviscaccia* and more derived taxa (Fig. 10, Node D) sharing only one unambiguous synapomorphy: position of the anterior border of mmpi below m1 (ch. 46[0]). This polytomy results from a lack of phylogenetic information (zero length branch) in the node that contains *Saremmys* + (*Eoviscaccia* + (Chinchillidae + Neopiblemyidae)), so in the consensus the node collapses. However, *Saremmys*

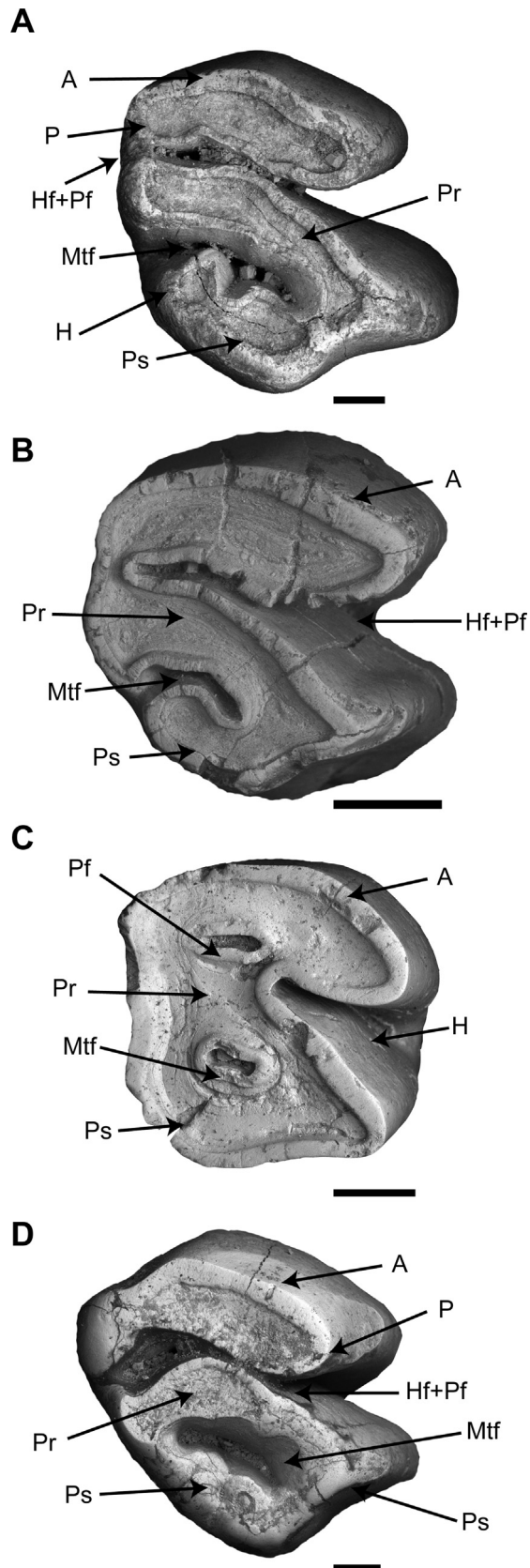


Fig. 9. Upper molars of *Saremmys ligcura*. A. MPEF-PV 11349B. B. MPEF-PV 5421. C. MPEF-PV 11348A. D. MPEF-PV 11349C. Scales are 500 μm in A and D and 1 mm in B and C.

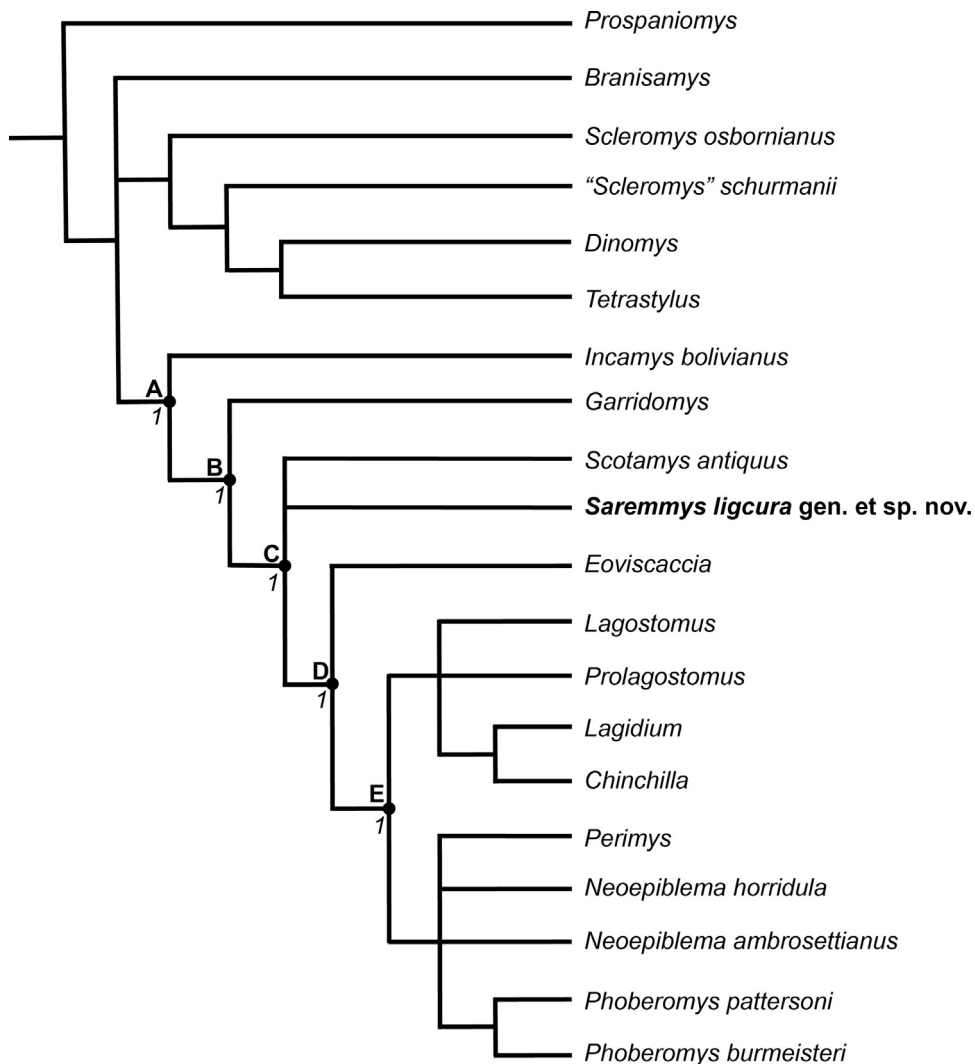


Fig. 10. Strict consensus of the most parsimonious trees (8 MPTs of 128 steps) recovered in the phylogenetic analysis. Upper case letters indicate the nodes, as described in the main text. The number below the nodes indicates the Bremer support values.

Fig. 10. Strict consensus des arbres les plus parcimonieux (8 MPTs de 128 pas) recueilli dans l'analyse phylogénétique. Les lettres en majuscules correspondent aux nœuds, comme l'indique le texte principal. Les chiffres sous les nœuds indiquent les valeurs de support de Bremer (1994).

differs from *Scotamys* in the absence of cement, a shorter root of the lower incisor, a more concave diastema and the distribution of the enamel, among the clear morphological differences of the tooth of both genera described above. *Saremmys* differs from *Eoviscaccia* + more derived taxa in the very thick width of the flexus/ids (ch. 7[1]), and the presence of two transverse crests on M1–M2 in adult stages (ch. 4[3]). Also, *Eoviscaccia* and the more derived taxa are more hypsodont, and with a clear tendency toward laminated teeth.

In the present contribution, we have included *Incamys bolivianus*, and *Scotamys antiquus* in the phylogenetic analysis. So far, *Scotamys* was never included in a phylogenetic

analysis and *Incamys* was only included in the analysis of [Rasia and Candela \(2018b\)](#).

Incamys bolivianus was considered a dasypsectid by several authors ([Lavocat, 1976](#); [Patterson and Wood, 1982](#)), although it was reassigned to Chinchilloidea by [Vucetich et al. \(2015a, 2015b\)](#). In this contribution, *Incamys* is recovered within Chinchilloidea, supporting [Vucetich et al. \(2015a, 2015b\)](#) and [Rasia and Candela \(2018b\)](#), and it is the most basal genus in the node towards Chinchillidae + Neoepiblemidae. In [Rasia and Candela \(2018b\)](#), *Incamys* is recovered as the most basal taxa in the node leading only to Chinchillidae. The basal position of *Incamys* (Fig. 10, Node A) is supported by the following

Fig. 9. Molaires supérieures de *Saremmys ligcura*. A. MPEF-PV 11349B. B. MPEF-PV 5421. C. MPEF-PV 11348A. D. MPEF-PV 11349C. Les barres d'échelle représentent 500 µm pour A et D et 1 mm pour B et C.

Table 1Dental measurements of the lower tooth of *Saremmys ligcura* (in mm).**Tableau 1**Mesures dentaires de la dent inférieure de *Saremmys ligcura* (en mm).

Material	p4			m1			m2			m3			Total	dp4		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	L	AW	PW
MPEF-PV 11341	3.98	2.44	3.22	3.91	3.38	3.33	3.82	3.47	3.40	3.97	3.58	2.86	15.68	–	–	–
MPEF-PV 11340	3.83	2.48	3.12	3.35	3.26	3.24	4.09	3.62	3.95	4.08	3.36	2.86	15.35	–	–	–
MPEF-PV 11342	–	–	–	3.93	3.25	3.55	3.86	3.30	3.13	3.05	3.43	2.79	10.84	–	–	–
MPEF-PV 5004	–	–	–	3.45	3.71	3.59	4.22	4.31	4.06	3.77	3.44	–	–	–	–	–
MPEF-PV 11343	–	–	–	4.15	3.27	3.29	4.33	3.54	3.05	–	–	–	–	–	–	–
MPEF-PV 11349E	3.83	2.14	2.93	–	–	–	–	–	–	–	–	–	–	–	–	–
MPEF-PV 5036A	–	–	–	3.77	3.16	2.67	–	–	–	–	–	–	–	–	–	–
MPEF-PV 5036A	3.91	2.11	3.09	–	–	–	–	–	–	–	–	–	–	–	–	–
MPEF-PV 5036A	3.90	2.54	3.19	–	–	–	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11346B	4.17	1.96	2.48	–	–	–	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11349D	4.09	2.24	2.98	–	–	–	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11345	4.13	2.20	3.29	–	–	–	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11347C	–	–	–	4.01	3.21	2.96	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11344	–	–	–	3.97	3.50	3.05	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11347D	–	–	–	3.62	3.07	3.01	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11347B	–	–	–	3.97	3.06	2.82	–	–	–	–	–	–	–	–	–	–
MPEF-PV 5036B	–	–	–	3.94	3.37	3.32	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11347A	–	–	–	4.37	3.76	3.71	–	–	–	–	–	–	–	–	–	–
MPEF-PV 5058	–	–	–	4.04	3.30	2.98	–	–	–	–	–	–	–	–	–	–
MPEF-PV 11349A	–	–	–	–	–	–	–	–	–	–	–	–	–	5.32	2.39	2.74
MPEF-PV 11348C	–	–	–	–	–	–	–	–	–	–	–	–	–	4.61	1.75	2.11
MPEF-PV 11346A	–	–	–	–	–	–	–	–	–	–	–	–	–	4.46	1.90	2.22
MPEF-PV 11348D	–	–	–	–	–	–	–	–	–	–	–	–	–	4.47	2.09	2.32
MPEF-PV 11348B	–	–	–	–	–	–	–	–	–	–	–	–	–	4.85	2.21	2.55

AW: anterior maximum preserved width; L: total preserved length; PW: posterior maximum preserved width; W: maximum preserved width.

unambiguous synapomorphies: the hypoflexus (in adults) extends more than half way across crowns (ch. 3[1]), the dorsal root of the zygoma is at the same level of M1–M2 (ch. 21[1]), a sagittal crest is present (ch. 27[0]).

Scotamys is recovered within Chinchilloidea as proposed by Loomis (1914) and Wood and Patterson (1959), unlike Vucetich (1985, 1989), who considered this genus a “cephalomyid”, and the proposal of Kramarz (2001b), Bertrand et al. (2012) and Vucetich et al. (2015a), who proposed the genus as a neoepiblemyid. The analysis of Busker and Dozo (2018) and Rasia and Candela (2018b) included “cephalomyids,” but did not include *Scotamys*, so future contributions should further test the position of this genus within the “cephalomyids”.

On the other hand, the position of *Garridomys* is supported by the following unambiguous synapomorphies: presence of cement (ch. 5[1]), posterior extension of the lower incisor below m3 (ch. 11[1]), and the fact that the anteroloph in M1–M3 reaches the paracone (ch. 48[1]).

4. Discussion

4.1.1. Taxonomic status and phylogenetic position of *Saremmys ligcura*

According to our phylogenetic results, *Saremmys* is deeply nested within Chinchilloidea as a Chinchilloidea incertae sedis (sensu Kerber et al., 2016; Kramarz et al., 2013; Rasia and Candela, 2018b; Vucetich et al., 2015a, 2015b), together with *Incamys*, *Scotamys*, and *Garridomys*. Although *Saremmys* forms a politomy with *Scotamys* and the more derived clade of chinchilloids, the combination of

Table 2Dental measurements of the superior tooth of *Saremmys ligcura* (in mm).**Tableau 2**Mesures dentaires de la dent supérieure de *Saremmys ligcura* (en mm).

Material	M1–2			M3		
	L	AW	PW	L	AW	PW
MPEF-PV 11348A	3.54	3.69	2.97	–	–	–
MPEF-PV 11349C	–	–	–	3.46	2.94	2.01
MPEF-PV 5036C	3.75	3.28	3.31	–	–	–
MPEF-PV 11349B	3.54	3.11	3.61	–	–	–
MPEF-PV 5421	3.33	3	2.44	–	–	–

AW: anterior maximum preserved width; L: total preserved length; PW: posterior maximum preserved width; W: maximum preserved width.

characters described above clearly justify the creation of a new genus and species (see § Phylogenetic analysis).

In recent publications (Kerber and Sánchez-Villagra, 2018; Kerber et al., 2017a, 2018; Kramarz et al., 2013; Rasia and Candela, 2018a, 2018b), *Garridomys* is placed as the sister group of a clade formed by *Eoviscaccia* and more derived chinchilloids. This result led the authors to interpret *Garridomys* as the earliest diverging chinchilloid within the clade that includes modern chinchillids (Kramarz et al., 2013). However, with the inclusion of *Incamys*, *Saremmys* and *Scotamys*, the evolutionary history is a little different. Our results indicate that *Incamys* is the most basal form of the lineage that leads to the origin of the modern vizcachas and chinchillas, whereas *Scotamys* and *Saremmys* are more closely related to *Eoviscaccia* and more derived forms. In this context, the position of *Garridomys* takes an intermediate place within this basal stock.

Eoviscaccia is recovered as sister taxa of Chinchillidae + Neoeplebimidae, similar to other recent analyses (Kerber and Sánchez-Villagra, 2018; Kerber et al., 2017a, 2018; Rasia and Candela, 2018a). In Rasia (2016) and Rasia and Candela (2018b), *Eoviscaccia* is recovered as a basal lineage within Chinchillidae. These proposals are different from the others authors, who considered the genus a Lagostominae (e.g., Bond et al., 1998; Kramarz, 2001b; Kramarz, 2005; Kramarz et al., 2013; Vucetich, 1989).

4.1.2. The diversity of Chinchilloidea in the Colhuehuapian SALMA

The record of new species *Saremmys ligcura* increases the knowledge of colhuehuapian chinchilloids, so far scarce and unique from Patagonia (Argentina) (Kramarz et al., 2013; Rasia and Candela, 2018b; Vucetich et al., 2010b, 2015a). The main localities with colhuehuapian chinchilloids are Gran Barranca, Bryn Gwyn, and Cerro Bandera, with a low diversity (only four genera known including *Saremmys*). It is interesting that more derived forms (*Eoviscaccia*, *Perimys*) coexisted with more basal forms (*Saremmys*, *Garridomys*) during the Colhuehuapian SALMA in these localities. It is also remarkable that *Eoviscaccia*, *Perimys*, and *Saremmys* are shared between Gran Barranca and Bryn Gwyn, while *Garridomys* so far is unique from Cerro Bandera (Neuquén). This discovery makes Bryn Gwyn and Gran Barranca the localities with the highest and more diverse record of colhuehuapian chinchilloids. It should be noted that the age of Cerro Bandera is still dubious (Busker et al., 2017; Kramarz et al., 2011; Kramarz et al., 2013, 2015), so the faunistic differences with Bryn Gwyn and the colhuehuapian levels of Gran Barranca could be due to chronological differences.

As stated above, *Saremmys* is one of the few taxa shared between Gran Barranca and Bryn Gwyn (Vucetich et al., 2010b), although, so far, it is clearly more abundant in Bryn Gwyn. Another genus very abundant in Bryn Gwyn and only represented by an isolated molar in Gran Barranca is *Soriamys* (Vucetich et al., 2010b). The efforts of prospection carried out over the years in both localities suggest that the difference in the abundance of taxa is not a bias of fieldwork. Also, the only specimen of *Saremmys* known from Gran Barranca is slightly smaller, which could be attributed to ecological differences between both localities (e.g., Arnal et al., 2017; Taraborelli et al., 2007). There are two main hypotheses that explain these size differences; one hypothesis proposes a chronological difference between Bryn Gwyn (Trelew Member) and Gran Barranca (Simpson, 1940). The other hypothesis proposes different environments for the two localities (Pérez, 2010; Pérez et al., 2010; Vucetich et al., 2010b). Despite the species is present in both localities, the clear difference in abundance of *S. ligcura* would support the ecological differences proposed for the localities. Nevertheless, to corroborate this hypothesis, a comparative integral study of the mammal assemblages of both communities would be necessary.

5. Conclusions

Here we present a new chinchilloid rodent, *Saremmys ligcura*, from the Chubut Province. *Saremmys ligcura* is the third genus of chinchilloids rodent from Bryn Gwyn and Gran Barranca and, like *Eoviscaccia* and *Perimys*, is shared by both localities. In general, the results of our phylogenetic analysis are consistent with those from previous studies and support the existence of several Chinchilloidea *incertae sedis*, including *S. ligcura*, and a supposed Tinguirirican SALMA (early Oligocene) for the origin of chinchilloids. Our results also support the inclusion of *Incamys* and *Scotamys* within Chinchilloidea *incertae sedis*, as proposed by previous authors. *S. ligcura* is part of the basal forms that led to the origin of the modern vizcachas and chinchillas. This finding increases our knowledge about the taxonomy and diversity of the Chinchilloidea *incertae sedis* during Colhuehuapian age, a key moment of the evolutionary history of the clade.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2019.05.003>.

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