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Neoreomys and *Scleromys* (Rodentia, Hystricognathi) from the Pinturas Formation, late Early Miocene of Patagonia, Argentina

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Abstract: The rodent genera *Neoreomys* and *Scleromys* Ameghino from the late Early Miocene Pinturas Formation (Ameghino´s «Astrapothericulan» beds) of Patagonia are here studied. A new species for each genus are recognized: *Neoreomys pinturensis sp. nov*., *Scleromys quadrangulatus sp. nov*. They are recorded exclusively in this unit and represent the oldest record of these genera. Both species differ from the typical Santacrucian species *N*. *australis* and *S*. *osbornianus*, respectively, by having less hypsodont cheek teeth with more persistent and larger flexi and flexids. These characters indicate a more primitive condition of their dentitions, and sug-gest they are their potential structural ancestors. *Neoreomys australis* and *Scleromys osbornianus* are also recorded in the Pinturas Formation, but they mostly occur in higher stratigraphic levels than their «Pinturan» counterparts.

Key words: Rodentia, *Neoreomys*, *Scleromys*, Systematics, Pinturas Formation, Miocene, Patagonia.

The Pinturas Formation is a continental Miocene unit exposed at the upper valley of the Pinturas River, west central Argentine Patagonia (Fig. 1) (Bown *et al.*, 1988). This unit bears a rich mammal assemblage first described by Ameghino (1906) as the «Astrapothericulan» fauna. Accord-ing to the evolutionary stage of this fauna, Ameghino (1900-1902, 1906), followed by Frenguelli (1931) and Castellanos (1937), concluded that these deposits are older than the Miocene coastal localities of the Santa Cruz Formation (Marshall, 1976) (Fig. 1), which typify the Santacrucian South American Land Mammal Age (SALMA; Simpson, 1940). Recent radiometric dates correlate both the Pinturas and the Santa Cruz Formations to the late Early Miocene (Fleagle *et al.*, 1995; Flynn & Swisher, 1995), but the $^{40}Ar/^{39}Ar$ date for the top of the middle sequence of the Pinturas Formation is older than dates given for all tuffs from the typical Santacrucian localities (Monte Observación and Monte León, Fig. 1) of the Santa Cruz Formation (Fleagle *et al.*, 1995). This correlation is also supported by biostratigraphic studies based on new and abundant fossil mammals derived from both the Pinturas and Santa Cruz formations (Bown & Fleagle, 1993; Kramarz & Bellosi, 2005; Kramarz & Bond, 2005).

This contribution completes a series of studies on the Hystricognath rodents derived from the Pinturas Formation (Kramarz, 2001a, 2002, 2004, 2006; Kramarz & Bellosi, 2005) . Fossil remains referable to the rodent genera *Scleromys* and *Neoreomys* from the Pinturas formation are herein examined. Both genera were originally described for the Santa Cruz Formation (Ameghino, 1887, 1891, 1894, Scott, 1905). De Barrio *et al.* (1984), Lich (1991), and Kramarz & Bellosi (2005) reported the occurrence of both taxa in the Pinturas Formation. New species are herein recognized and other known species are revised in order to analyze their taxonomic sta-tus and to evaluate their relationships with those known from other Oligocene and Miocene Faunas.

TERMINOLOGY

Nomenclature of occlusal structures of the upper molars generally follows Wood & Patterson (1959) and Patterson & Wood (1982), except that the third crest is termed the mesoloph and its associated labial cusp is termed the mesostyle (Hoffstetter, 1975; Lavocat, 1976; Vucetich & Verzi, 1994; Candela, 1999). Nomenclature of the lower cheek teeth also generally follows Wood & Patterson (1959) and Patterson & Wood (1982), except that the second crest of the molars and the third crest of the deciduous premolars are termed the mesolophid (Lavocat, 1976; Candela, 1998, 2002). Muscular terminology follows Woods & Howland (1979).

Institutional Abbreviations. **MACN A**, Colección Nacional Ameghino, Museo Argentino de Ciencias Naturales «B. Rivadavia»; **MACN Pv**, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales «B. Rivadavia»; **MLP**, Museo de La Plata.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Superfamily CAVIOIDEA Kraglievich, 1930
Family DASYPROCTIDAE Smith, 1842

Genus ***Neoreomys*** Ameghino, 1887

Type species. Neoreomys australis Ameghino, 1887

Referred species. The type species and *Neoreomys huilensis* Fields, 1957; *Neoreomys pinturensis sp. nov.*

Geographic and stratigraphic distribution. Pinturas Formation (late Early Miocene) Santa Cruz province; Santa Cruz Formation, Santacrucian SALMA (late Early Miocene), Santa Cruz and Chubut provinces; Collón Cura Formation, Colloncuran SALMA (Middle Miocene), Río Negro and Neuquén provinces, Argentina. La Victoria Formation, Laventan SALMA (late Middle Miocene), Colombia.

Neoreomys australis Ameghino, 1887

Neoreomys decisus Ameghino, 1887:11
Neoreomys indivisus Ameghino, 1887: 11
Neoreomys variegatus Ameghino, 1894: 324–325
Neoreomys (*Pseudoneoreomys*) *leptorhynchus* Ameghino, 1891:301
Neoreomys (*Pseudoneoreomys*) *mesorhynchus* Ameghino, 1891:301
Neoreomys (*Pseudoneoreomys*) *pachyrhynchus* Ameghino, 1891:300

Holotype. MLP 15–121, right mandibular fragment with p4 – m2 and incisor.

Referred materials from Pinturas Formation. See appendix.

Stratigraphic and geographic provenance. MACN Pv SC2222 comes from Portezuelo Sumich Norte; MACN Pv SC2865 comes from Loma de la Lluvia; MACN Pv SC3977 and 4013 come from Ea. Ana María; MACN Pv SC2540 and 2840 from Ea. Los Toldos Norte; MACN Pv SC2830, 2831 and 3441 from Ea. Los Toldos Sur; MACN Pv SC4031 from Ea. La Cañada; MACN Pv SC4043, 4056, 4061, and 4062 from Gobernador Gregores; MACN Pv SC4067, 4076, 4085, and 4086 from Lago Cardiel (for the stratigraphic posi-tion of these localities see Bown & Larriestra, 1990 and Bown & Fleagle, 1993).

FIG. 1. Location map. **1**, Area of the upper val-ley of Pinturas River; **2**, Estancia La Cañada; **3**, Monte León; **4**, Monte Observación.

Comments. Ameghino recognized nine species of *Neoreomys* (grouped into the subgenera *Neoreomys* and *Pseudoneoreomys*), all from the Santa Cruz Formation. Scott (1905) proposed that only the type species, *N. pachyrhynchus* Ameghino 1891, *N. decisus* Ameghino 1887, and *N. variegatus* Ameghino 1894 are valid. Fields (1957) concluded that the differences among these species are not significant, and that *N. australis* is the unique Santacrucian valid species. We follow Fields' proposal, as we interpret that the differences in size and morphology among the specimens of *Neoreomys* derived from the Santa Cruz Formation are the consequence of ontogenetic variations.

Neoreomys pinturensis sp. nov.
(Figs. 2A–F)

Etymology. In reference to the Pinturas River.

Holotype. MACN Pv SC2211, right mandibular fragment with m1 or m2 (Fig. 2E).

Paratype. MACN Pv SC2177, right m3; MACN Pv SC2212, right p4; MACN Pv SC2174, left M1 or M2; MACN Pv SC2175, right M1 or M2, and MACN Pv SC2176, right M1 or M2.

Hypodigm. The holotype, the paratype, and the specimens listed in the appendix.

Stratigraphic and geographic provenance. MACN 4103 comes from Carmen lower; the remaining specimens come from Portezuelo Sumich Norte (see Bown & Larriestra, 1990).

Diagnosis. Cheek teeth similar in size to those of *N. australis*; nearly 50% larger than in *N. huilensis*. Cheek teeth lower crowned than in *N. australis*. As in *N. huilensis*, molars with fossettes and fossettids more persistent, hypoflexus/id less penetrating, mesofossette/id wider, and mesoloph and mesolophid broader and longer than in *N. australis*.

Description and comparisons. Cheek teeth of *N. pinturensis* have nearly the same size as those of *N. australis* (Table 1), which are significantly larger than in *N*. *huilensis* (Laventan SALMA). The available cheek teeth are lower crowned than those of *N*. *australis* in a comparable stage of wear (compare Fig. 2G with 2H and Fig. 2I with 2J).

The upper molars (Fig. 2A–C) have the same pentalophodont occlusal pattern as *N*. *australis* (Fig. 2H), but the labial flexi are wider and longer, specially the mesoflexus – mesofossette, which extends up to the center of the crown. The fossettes persist until more advanced stages of wear (specially the posterofossette). The hypoflexus is less penetrating and it remains united to the anterofossette until more advanced stages of wear than in *N*. *australis*. The mesoloph is wider and longer, thus the occlusal configuration is more similar to that of *Australoprocta* (Kra-marz, 1998), from the Colhuehuapian SALMA, than to *N*. *australis*.

Similarly, the lower cheek teeth (Fig. 2D–F) have wider and more penetrating lingual flexids, in particular the mesoflexid – mesofossettid. The ectolophid is very short and the mesolophid is as thick as the adjacent crest, and it extends transversely more than half of the width of the crown in all the cheek teeth, even in the m3 (Fig. 2D), as in *N. huilensis*. On the contrary, in *N*. *australis* the ectolophid is gradually longer from the m1 toward the m3; the mesolophid is shorter and appears as a derivation of the lingual end of the ectolophid, with the consequent reduction of the mesofossettid. The anterolophid of moderately worn teeth of *N*. *pinturensis* have a posterior projection, as it occurs very occasionally in *N*. *australis*.

TABLE 1. Summary of tooth measurements for *Neoreomys pinturensis sp. nov*. in millimeters. **Abbreviations**: **APL**, anteroposterior length; **n**, number of specimens; **TRW**, transverse width; **SD**, standard deviation.

		M1 or M2	p4	m1 or m2	m3
n		5	3	7	3
APL	mean	5.76	7.47	6.00	6.13
	range	0.50	1.50	1.30	1.00
	SD	0.24	0.84	0.45	0.55
TRW	mean	5.88	5.50	5.63	5.83
	range	1.40	0.80	0.80	0.30
	SD	0.58	0.44	0.29	0.21

Discussion. The cheek teeth of *N. pinturensis* are positively lower crowned, and therefore more primitive, than those of *N*. *australis* (the rela-tive degree of hypsodonty of *N*. *huilensis* is unknown). They also differ by having more penetrating hypoflexus and hypoflexid and less ephemeral fossettes and fossettids; such characters are related to a later occlusal simplification than in *N*. *australis*, which is associated to the lesser degree of hypsodonty (Schmidt- Kittler, 1984) . *Neoremys pinturensis* also differs by having a well developed mesoloph and mesolophid, as in *N*. *huilensis*. This feature seems to be also related to the hypsodonty, at least among the Patagonian dasyproctids, since *Australoprocta*, *Neoreomys australis,* and *Alloiomys* Vucetich, 1979 (Colloncuran SALMA, Middle Miocene) represent a gradient of increasing hypsodonty and of a parallel reduction of the mesoloph and mesolophid.

The posterior projection of the anterolophid is variably present in other cavioids: it is com-pletely developed in living dasyproctids, sporadic in *Luantus*, *Australoprocta*, and *Neoreomys australis*, and absent in *Incamys*, *Scleromys*, and *Branisamys*. This structure could be interpreted as a rudiment of a «neolophid», considered as a derived structure for all the South American Hystricognathi (Patterson & Wood, 1982), or at least for the Erethizontoidea (Candela, 1998). However, a posterior projection of the anterolophid is variably present in primitive octodontoids (e.g., *Platypittamys* Wood, *Migraveramus* Patterson & Wood, *Caviocricetus* Vucetich & Verzi, *Galileomys* Vucetich & Kramarz), suggesting that the polarity of this feature is dubious and it must be revised within a broader evolutionary context.

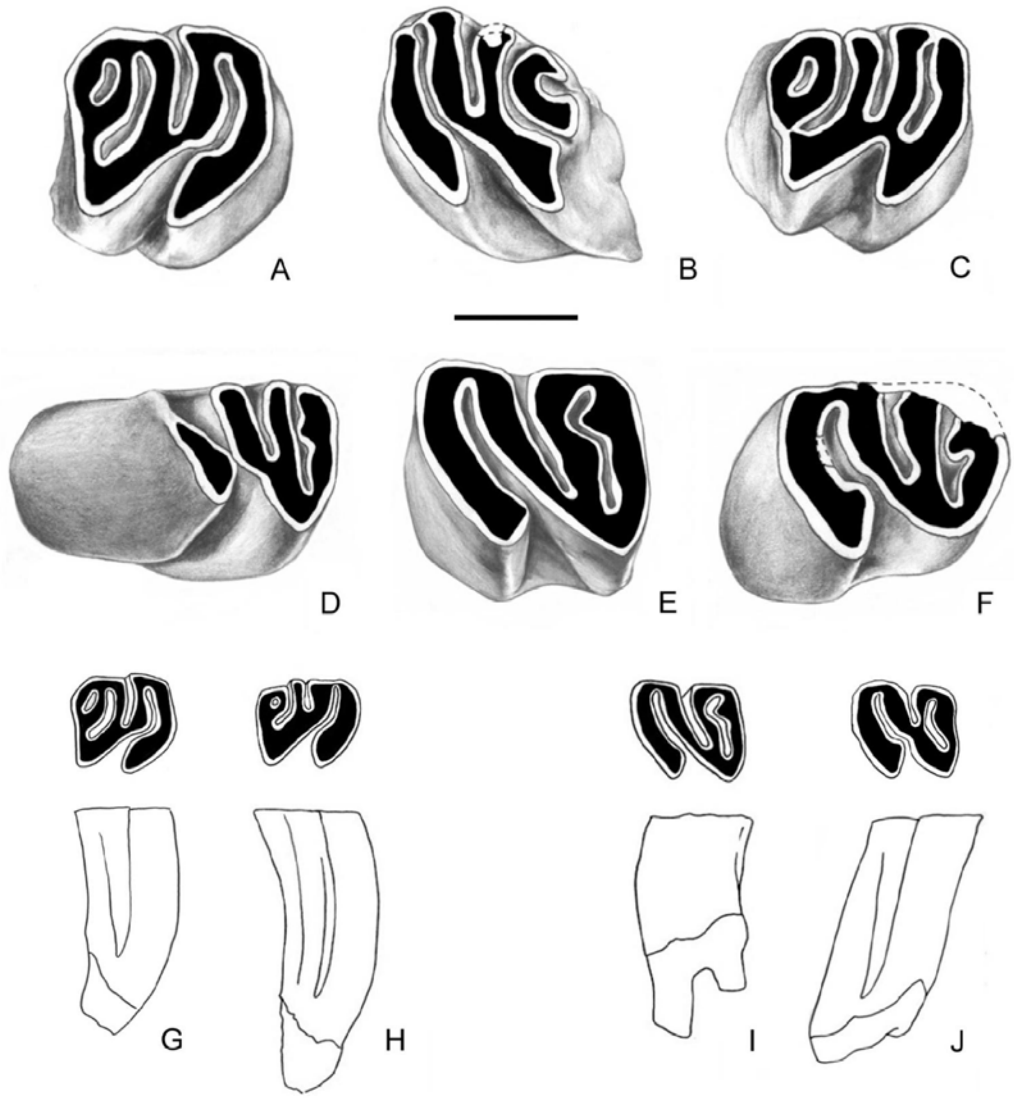

FIG. 2. Cheek teeth of *Neoreomys spp*. **A**–**G**, **I**: *Neoreomys pinturensis sp. nov*., from Pinturas Formation; **H** and **J**: *Neoreomys australis* from Santa Cruz Formation. **A**: MACN Pv SC2175, right upper molar. **B**: MACN Pv SC2174, left upper molar. **C**: MACN Pv SC2176, right upper molar. **D**: MACN Pv SC2177, right m3. **E**: MACN Pv SC2211, (holotype of *N. pinturensis*), right m1 or m2. **F**: MACN Pv SC2212, right p4. **G**: idem A, in schematic occlusal and lingual view. **H**: right upper molar, in schematic occlusal and lingual view. **I**: idem E, in schematic occlusal and labial view. **J**: Right m1 or m2, in schematic occlusal and lingual view. Scale bar equals 5 mm.

Family DINOMYIDAE, Alston 1876

The relationships of the Dinomyidae with the main histricognath groups are still controversial; some evidences relate them to the Erethizontidae (Ray 1958) or to the Chinchillidae (Huchon & Douzery 2001). Dinomyids are here tentatively classified within the Cavioidea, following Simpson (1945), Patterson & Wood (1982), and McKenna & Bell (1997), until further evidence is known.

Genus ***Scleromys*** Ameghino, 1887

Neoreomys Ameghino, 1887 (in part)
Lomomys Ameghino, 1891

Type species. Scleromys angustus Ameghino, 1887

Referred species. The type species and *Scleromys osbornianus* Ameghino, 1894; *Scleromys quadrangulatus sp. nov.*

Geographic and stratigraphic distribution. Pinturas Formation and Santa Cruz Formation, Santacrucian SALMA (late Early Miocene), Santa Cruz province, Argentina.

Remarks. The genus *Scleromys* was referred to the Echinomyidae (=Echimyidae) by Ameghino (1889), to the Myocastoridae by Scott (1905), to the Dinomyidae by Fields (1957), and to the Dasyproctidae by Patterson & Wood (1982). We follow Field´s proposal by virtue of *Scleromys* seems to be closely related to Laventan dinomyids «*Scleromys*» *schurmanni* and «*Scleromys*» *colombianus*, although they probably are not co-generic with the Santacrucian species of *Scleromys* according to Patterson & Wood (1982) and Walton (1996).

Nomenclatural discussion. Ameghino based *S. angustus* upon a left mandibular ramus with p4–m2, which altogether have a complete length of 17 mm (at present lost in MLP collections), briefly described in 1887. In 1889 Ameghino en-larged the description of this specimen and pro-vided more detailed dental measurements; he also referred one isolated m3 with 6,5 mm in length and 5,3 mm in width (Fig. 3A), and one isolated upper molar (MACN A 1681–82; both figured in Ameghino, 1889: pl. 7, figs. 21 and 22; the upper would correspond to a very worn mo-lar of *Neoreomys*) . Thus, the deduced complete length for p4–m3 of *S. angustus* is nearly 23,5 mm. In 1891 Ameghino described a palate with dentition referred to this species, with a complete P4–M3 length of 16,5 mm. This measurement, which is even shorter than the p4–m2 length of the holotype, was probably taken from the MACN A 4361 (at present labeled as holotype of *S. angustus*), since this is the only specimen in the MACN Ameghino Collection with preserved pal-ate. In 1894 Ameghino described *S. osbornianus*, indicating that the total length for p4–m3 was 22 mm, and that this species is more robust than the type species. Such assertion suggests that Ameghino did not compare *S*. *osbornianus* with the MLP specimen described in 1887. As Ame-ghino was denied to compare specimens housed in MLP collections after 1888 (see Wood & Patterson, 1959:367), henceforth he probably based his conception of *S* . *angustus* on a new specimen selected from his own collection (prob-ably the MACN A 4361). Scott (1905) suggested that *S. osbornianus* is not valid, pointing out that the size of the teeth is equal or slightly greater than in *S. angustus*. The measurement for p4– m3 length of *S. angustus* given by Scott is 20 mm, taken from a specimen in Ameghino Collection. This length nearly agrees with that of the lower dentition of the MACN A 4361 (Fig. 3B). We in-terpret that Scott considered the MACN A 4361 as representative of *S*. *angustus*, and he neither compared the MLP holotype.

The revision of all available specimens from MLP and MACN collections reveals that both Santacrucian species of *Scleromys* are valid and well differentiated. *Scleromys angustus* is the largest species and it is known only by the iso-lated m3 (MACN A 1682) figured by Ameghino (1889), and by two specimens from the MLP col-lection (MLP 15–204 and 15–379). The remain-ing specimens derived from the Santa Cruz For-mation, including the MACN A 4361, are refer-able to *S. osbornianus*, the smallest and better-known species. The type specimens of *Neoreomys insulatus* Ameghino and *Neoreomys limatus* Ameghino are also referable to *S*. *osbornianus*. A comparison of the dental measurements for the species of *Scleromys* is shown in Table 2.

Scleromys osbornianus Ameghino, 1894

Neoreomys insulatus Ameghino, 1889:138
Neoreomys limatus Ameghino, 1891:142

Holotype. MACN A 10121, an incomplete skull with left P4–M3 and the incisors

Referred materials from Pinturas Formation. see appendix.

Stratigraphic and geographic provenance. MACN Pv SC2070–2072, 3434, 3439, 3440, and 3442 come from Los Toldos Sur; MACN Pv SC4044 and 4064 come from Gobernador Gre-gores; MACN Pv SC4072 comes from Lago Cardiel; MACN Pv SC4104 comes from Estancia Ana María (see Bown & Larriestra, 1990; Bown & Fleagle, 1993).

Comments. These specimens are here referred to *S. osbornianus* because they agree in size with the holotype and with the measurements of the specimens referred by Scott (1905). *Scleromys osbornianus* was previously known only for the Santa Cruz Formation.

Scleromys quadrangulatus sp. nov.
(Figs. 3C–E)

Scleromys sp. (de Barrio *et al.*, 1984)

Etymology. In reference to the quadrangular contour of its lower molars.

Holotype. MLP 82–VI–3–2; right mandibular fragment with complete dentition (Fig. 3C).

Hypodigm. The holotype and the specimens listed in the appendix.

Stratigraphic and geographic provenance. The holotype comes from the «Astrapothericulan beds», from an undetermined level and locality

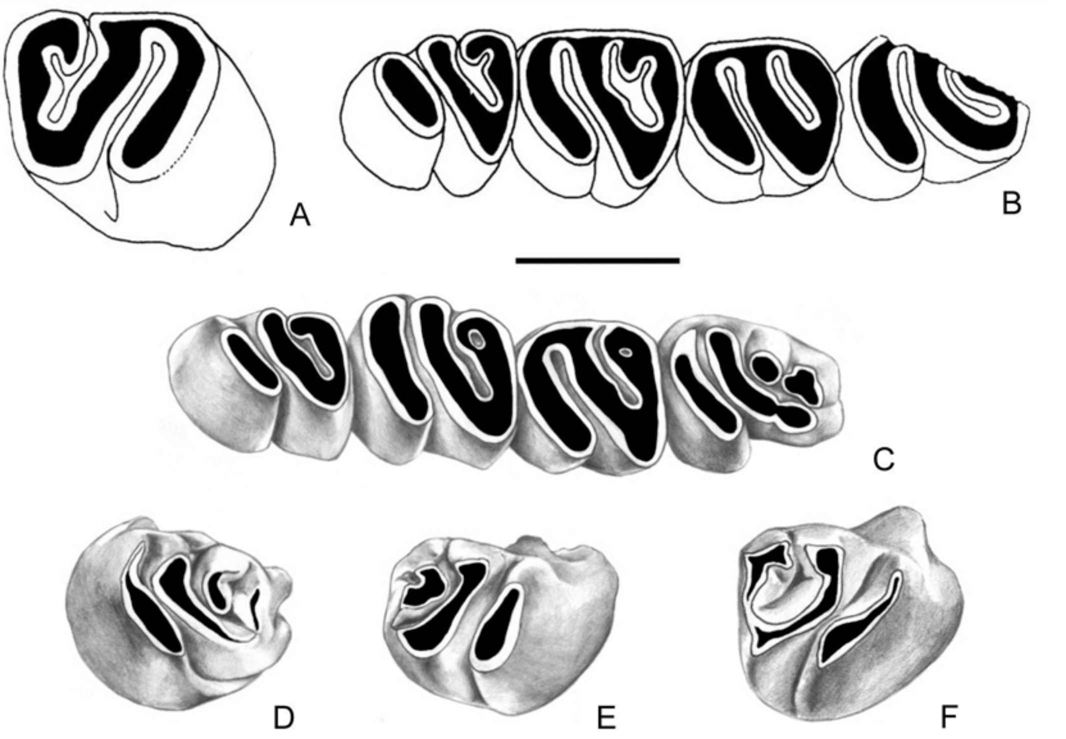

FIG. 3. Compared dentitions of *Scleromys* spp. in occlusal view. **A**: *Scleromys angustus,* from Santa Cruz Formation; **B** and **F**: *Scleromys osbornianus*, from Santa Cruz Formation; **C**-**E**: *Scleromys quadrangulatus sp. nov*., from Pinturas Formation. **A**: MACN A 1681, left lower molar. **B**: MACN A 4362, right p4 – m3 (reversed). **C**: MLP 82–VI–3–2 (holotype of *Scleromys quadrangulatus sp. nov*.), right p4 – m3. **D**: MACN Pv SC3822, right upper molar. **E**: MACN Pv SC3839, right P4. **F**: MACN Pv SC3840, right P4. Scale bar equals 5 mm.

next to the valley of Pinturas River (de Barrio *et al.*, 1984); MACN Pv SC2080 – 2083, 2113 – 2116, 3433, and 3435 come from Ea. El Carmen lower; MACN Pv SC2224 – 2232, and 3438 from Portezuelo Sumich Norte; MACN Pv SC2439, 2430, and 3822 from Cerro de los Monos; MACN Pv SC2841 and 2842 from Los Toldos Norte; MACN Pv SC2866 – 2867 from Loma de la Lluvia; MACN Pv SC3839 and 3972 – 3974 from Ea. Ana María, MACN Pv SC2061 from Portezuelo Sumich Sur (see Bown & Larriestra, 1990).

Diagnosis. Cheek teeth more than 10% smaller than in *S*. *angustus*, similar to *S. osbornianus*, but the lowers with more quadrangular contours. Fossettes and fossettids larger and more persistent than in the *S. osbornianus*, specially the anterofossettid. Upper unworn molars with vestigial mesostyle. P4 with posterofossette present in juvenile stages, as in «*Scleromys*» *colombianus* and «*Scleromys*» *schurmanni*. Lower premolars with a flexid on the anterior wall in young specimens, as in «*Scleromys*» *colombianus*.

Description and Comparison. The teeth of *Scleromys quadrangulatus* are similar in size to those of *S. osbornianus* and smaller than those of *S*. *angustus* (Tables 2, 3). The Lower molars (Fig. 3C) have quadrangular outlines, with the anterior borders usually straight, but with variations depending on the stage of wear. On the contrary, in *S. osbornianus* (Fig. 3B) the ante-rior margins of the lower molars are convex, thus the teeth have more ovoid contours. The occlu-sal morphology shows the typical 'S' shape pat-tern of the genus, but the anterofossettid is comparatively larger and persists until more advanced stages of wear than in *S. osbornianus*. The mesolophid is reduced and the anterofossettid is undefined in the m3 of the holotype (Fig. 3C), but in other specimens the m3 has the same con-dition as in m1 and m2.

Lower premolars are longer than molars and with the trigonid narrower than the talonid.

Unworn or little worn p4 (Fig. 3C) have three distinguishable cups on the anterior portion of the tooth: the protoconid (anterolabial), the metaconid (anterolingual), and a voluminous cusp (probably corresponding to the mesostylid) posterior to the anterolingual cusp. The metaco-nid is isolated from the protoconid by a shallow anterior flexid, as in young specimens of «*S*». *colombianus* (see Fields 1957:fig. 14a 1), but not in *S. osbornianus*. The metaconid has a poste-rior spur that does not reach the «mesostylid» during early stages of wear; the flexid between both cusps is deeper than in *S. osbornianus*. Worn p4s do not show significant differences with those of *S. osbornianus*.

The upper molars (Figs. 3D) have more per-sistent posterofossette than in *S. osbornianus* but more ephemeral than in «*S*». *schurmanni* and «*S*». *colombianus*, and it is usually connected with the metafossette. Unworn or little worn specimens (Fig. 3D) have a small protuberance on the labial margin between the paracone and the metacone. This structure can be interpreted as a vestigial mesostyle, and it is not present in specimens referable to *S. osbornianus* in the same stage of wear. The P4 (Fig. 3E) has more quad-rangular contour and a differentiable «metaloph» and «metafossette» during the initial stages of wear, in opposition to those of *S. osbornianus* (Fig. 3F).

The mandibular ramus has the pit for the in-sertion of the tendon of the *masseter medialis pars infraorbitalis* shallower than in *S. osbor-nianus*. There is a small accessory foramen pos-terior to the mental foramen, which is also ob-served in some specimens referable to *S. osbor-nianus* . The remaining characters of the pre-served part of the jaw and of the lower incisor are similar to those of *S. osbornianus*.

Discussion. The molars of *S. quadrangulatus* have nearly the same size as those of *S. osbornianus* (the total length p4–m3 of the holotype is 21,5 mm.). The most conspicuous dif-ference is the more quadrangular contours of the molars, as in *S*. *angustus*, and the larger trans-verse extension and persistence of the antero-fossettid in the lower molars and of the poste-rofossette in the uppers. Likewise, the mesostyle in the upper molars and the «metaloph» and «metafossette» in the P4 are also retained, at least in juvenile stages. The persistence of these structures produces the retention of a complex occlusal morphology until more advanced stages of wear than in *S. angustus* and *S. osbornianus*. Thus, the cheek teeth of *S. quadrangulatus* rep-resent a more primitive stage in the process of occlusal simplification, characteristic of the

TABLE 2. Compared dental measurements (in mm) for *S. osbornianus*, *S. quadrangulatus sp. nov*. and *S. angustus*. **Abbreviations**: **n**, number of specimens; **SD**, standard deviation.

Species		Lenght p4-m3	Lenght p4-m2	Lenght M1-M3
S. osbor-	n	6	11	3
nianus	mean	19.80	14.80	12.60
	SD	1.01	0.29	0.36
	n	3	4	–
S. quadran-	mean	20.87	15.08	–
gulatus	SD	1.07	0.86	–
	n	1	1	1
S. angustus	mean	23.50	17.00	16.70

cavioids of the patagonian radiation. Laventan dinomyids «*Scleromys*» *schurmanni* and «*Scle-romys*» *colombianus* have molars with even more quadrangular contours and larger and more per-sistent fossettes and fossettids than *S. qua-drangulatus*. However, Laventan species would represent a phyletic line in which ancestral oc-clusal structures are retained but with a novel disposition, that preannounce the characteristic multilaminar pattern of the more advanced dinomyids (e.g., *Eumegamys*, *Tetrastylus*, etc.) (Fields, 1957).

Vucetich & Kramarz (2003) interpreted that the presence of a flexid on the anterior wall of the p4 is the consequence of the absence of an anterior cingulum, and stated that it is a plesiomorphic character for the Octodontoidea, since it occurs in the Oligocene phiomorh *Phiomys andrewsi* and in primitive octodontoids as *Deseadomys*, *Sallamys*, and *Galileomys*. An ephemeral flexid is also observed in juvenile specimens of the primitive chinchilloids *Cephalomys*, *Scottamys*, and *Eoviscaccia* and in the primitive eocardiid *Chubutomys* (Wood & Patterson, 1959; Kramarz, 2001b), suggesting that this character is primitive for all the Hystricognathi.

CONCLUSIONS

A new species of *Neoreomys* and of *Scleromys* are herein recognized for the Pinturas Forma-tion; both are recorded exclusively in this unit representing the oldest record of these genera. *Neoreomys pinturensis sp. nov*. differs from *N. australis* (the only Santacrucian valid species of the genus) by having lower crowned cheek teeth and more persistent and larger flexi and flexids.

TABLE 3. Summary of tooth measurements for *Scleromys quadrangulatus sp. nov*. in millimeters. **Abbreviations**: **APL**, anteroposterior length; **n**, number of specimens; **TRW**, transverse width; **SD**, standard deviation.

		DP4	P4	M1	M2	M1 or 2	M3	dp4	p4	m1	m2	m1 or 2	m3	i1
n		4	14	5	3	16	17	5	20	5	8	27	21	3
APL	mean	4.80	4.63	4.44	4.67	4.66	5.00	6.30	6.09	4.84	4.99	5.11	5.41	4.53
	range	0.60	0.50	0.50	0.20	0.70	0.20	0.60	1.20	0.80	0.80	0.80	1.00	0.90
	SD	0.42	0.16	0.18	0.12	0.21	0.06	0.42	0.38	0.30	0.25	0.21	0.29	0.45
TRW	mean	4.05	4.96	4.48	5.00	4.78	4.66	3.85	4.67	4.82	5.07	4.86	4.79	4.20
	range	0.10	0.10	0.60	0.20	1.30	0.80	0.30	0.80	0.80	1.00	1.30	1.20	0.90
	SD	0.07	0.05	0.28	0.10	0.44	0.30	0.21	0.32	0.31	0.35	0.38	0.34	0.46

S. quadrangulatus differs from *S. osbornianus* (the smallest and more abundant Santacrucian spe-cies of the genus) by having more quadrangular lower molars, more persistent and larger flexi and flexids, and P4 with more complex occlusal pat-tern, resembling Laventan dinomyids. The pres-ence of a flexid on the anterior wall of the p4 in *S*. *quadrangulatus* (unworn or little worn p4 of *N*. *pinturensis* is unknown), also reveals a more primitive condition. At least from the dental point of view, these species can be interpreted as struc-tural ancestors of their respective Santacrucian counterparts.

The typical Santacrucian species *N*. *australis* and *S*. *osbornianus* are also recorded in the Pinturas Formation. The examination of their stratigraphic distribution reveals that *S*. *osbornianus* occurs at those localities where the fossil bearing level were not precisely located in the column through lithological comparisons (Los Toldos, La Cañada, Gobernador Gregores, and Lago Cardiel) (Bown & Larriestra, 1990; Bown & Fleagle, 1993), but interpreted as correspond-ing to the upper sequence according to their faunal association (Kramarz & Bellosi, 2005). *S*. *quadrangulatus* is recorded exclusively from those localities correlated to the lower and mid-dle sequences of this unit (Kramarz & Bellosi, 2005:fig. 4). *N*. *australis* is recorded in the mid-dle sequence and at those localities interpreted as corresponding to the upper sequence. *N*. *pinturensis* occurs in the lower sequence and in the lowermost part of the middle sequence of the formation. Therefore, the Santacrucian species almost do not coexist in the same stratigraphic levels with their more primitive «Pinturan» al-lies.

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APPENDIX

List of specimens referred to *Neoreomys pinturensis sp. nov*. MACN Pv SC2213, right M1 or M2; MACN Pv SC2214, left M1 or M2; MACN Pv SC2215, left m1 or m2; MACN Pv SC2216, right m1 or m2; MACN Pv SC2217, right M1 or M2; MACN Pv SC2218, two right m3; MACN Pv SC2219, two left m1 or m2; MACN Pv SC2220, 2 upper molars; MACN Pv SC2221, left p4; MACN Pv SC3437, right m1 or m2 and MACN Pv SC4103, upper molar.

List of specimens from the Pinturas Formation referred to *Neoreomys australis* Ameghino. MACN Pv SC2222, 4 cheek teeth; MACN Pv SC2540, 2 cheek teeth; MACN Pv SC2830; 40 upper cheek teeth; MACN Pv SC2831, 32 lower cheek teeth; MACN Pv SC2840, 4 cheek teeth; MACN Pv SC2865, upper molar; MACN Pv SC3441, left maxillary fragment with P4–M2; MACN Pv SC3977, 13 cheek teeth; MACN Pv SC4013, cheek tooth; MACN Pv SC4031, 4 cheek teeth; MACN Pv SC4043, 2 cheek teeth; MACN Pv SC4056, 3 cheek teeth; MACN Pv SC4061, left mandibular fragment with m2; MACN Pv SC4062, 2 cheek teeth; MACN Pv SC4067, left mandibular fragment with p4–m3 and 6 cheek teeth; MACN Pv SC4076, 3 cheek teeth; MACN Pv SC4085, 3 cheek teeth; MACN Pv SC4086, 7 cheek teeth.

List of specimens referred to *Scleromys quadrangulatus sp. nov*. MACN Pv SC2061, right M3; MACN Pv SC2080, left maxillary fragment with M1–M2; MACN Pv SC2081, left maxillary fragment with M3; MACN Pv SC2082, left mandibular fragment with dp4–m1; MACN Pv SC2083, right mandibular fragment with m3; MACN Pv SC2113, left m2; MACN Pv SC2114, left M1 or M2; MACN Pv SC2115, left M3, MACN Pv SC2116, 7 cheek teeth; MACN Pv SC2224, left m3; MACN Pv SC2225, right m1 or m2; MACN Pv SC2226, left mandibular fragment with m2–m3; MACN Pv SC2227, right maxillary fragment with DP4–M1; MACN Pv SC2228, right upper molar; MACN Pv SC2229, right P4; MACN Pv SC2230, left maxillary fragment with DP4–M1; MACN Pv SC2231, left maxil-lary fragment with P4–M2; MACN Pv SC2232, 26 cheek teeth; MACN Pv SC2429, right mandibular fragment with m1; MACN Pv SC2430, 7 cheek teeth; MACN Pv SC2841, left maxillary fragment with P4–M1; MACN Pv SC2842, right M1 or M2; MACN Pv SC2866, left m3; MACN Pv SC2867, 14 cheek teeth; MACN Pv SC3433, right mandibular fragment with p4–m1; MACN Pv SC3435, left maxillary fragment with M1–M3; MACN Pv SC3438, right mandibular fragment with dp4–m1, MACN Pv SC3822, left M3; MACN Pv SC3839, right P4; MACN Pv SC3972, left mandibular fragment with p4–m2; MACN Pv SC3973, right P4; MACN Pv SC3974, 25 cheek teeth.

List of specimens from the Pinturas Formation referred to *Scleromys osbornianus* Ameghino. MACN Pv SC2770, right mandibular fragment with dp4–m1; MACN Pv SC2771, right mandibular fragment with m3; MACN Pv SC2772, 59 cheek teeth; MACN Pv SC3434, left mandibu-lar fragment with p4–m2; MACN Pv SC3439, left mandibular fragment with p4–m1; MACN Pv SC3440, right mandibular fragment with p4–m2; MACN Pv SC3442, right mandibular fragment with m1–m2, MACN Pv SC4044, lower molar; MACN Pv SC4064, lower molar; MACN Pv SC4072, right upper molar; MACN Pv SC4104, upper molar.