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## Original article

# A new species of *Chubutomys* (Rodentia, Hystricognathi) from the late Oligocene of Patagonia and its implications on the early evolutionary history of Caviioidea sensu stricto<sup>☆</sup>

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## ABSTRACT

Caviioidea is represented today by Dasyproctidae (agouties), Cuniculidae (pacas), and Caviidae (cavies or “guinea pigs”, maras, mocos, and capybaras). Caviioidea sensu stricto (Caviioidea s.s.) clusters the extant and extinct Caviidae together with a diverse assemblage of extinct taxa grouped in the family Eocardiidae. Recent phylogenetic analyses of this group based on morphological characters corroborated the monophyly of Caviioidea s.s., but retrieved a paraphyletic arrangement of “eocardiids” as successive sister taxa of the crown-group Caviidae. The late Oligocene (Deseadan South American Land Mammal Age, SALMA) record of Caviioidea s.s. is relevant because it represents the oldest occurrence of the group, represented only by very scarce materials of *Asteromys punctus* and *Chubutomys simpsoni*. New materials of Deseadan cavioids are of prime importance to understand the early evolution of this group. The locality of Punta Nava (northeastern Santa Cruz Province, Patagonia, Argentina) has yielded a fauna assigned to the Deseadan SALMA, but no rodent remains were known so far. A recent fieldwork in this locality provided the first findings of fossil caviomorphs, including remains of Caviioidea, Octodontidae, Chinchilloidea, and Erethizontoidea. A new species of Caviioidea s.s. from this locality is here described, and its phylogenetic affinities are evaluated. This new cavioid from the Deseadan SALMA, and the reinterpretation of the morphology of *Chubutomys simpsoni*, provide new insights into the early diversification of Caviioidea s.s. The new species from the late Oligocene, and the high position of *Chubutomys* in the phylogeny, draw back the origin of all protohypodont lineages of Caviioidea s.s. to the Deseadan SALMA. Furthermore, this suggests that the early evolution of Caviioidea s.s. occurred through a major diversification pulse larger than previously proposed.

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## 1. Introduction

Within South American hystricognath rodents (i.e., Caviomorpha sensu Wood, 1955), the superfamily Caviioidea is represented today by Dasyproctidae (agouties), Cuniculidae (pacas), and Caviidae (cavies or “guinea pigs”, maras, mocos, and capybaras). Caviomorphs of this divergent group currently thrive in different ecosystems throughout South America (e.g., semiaquatic, dry steppes, forest edges, rocky ledges; Woods, 1984), showing diverse behavioral habits (Rowe and Honeycutt, 2002). They have a broad range of body size, from the minute *Microcavia* (approx. 300 gr) to the giant *Hydrochoerus* (up to 80 kg), the largest living rodent

(Mares and Ojeda, 1982; Woods, 1984; Eisenberg and Redford, 2000).

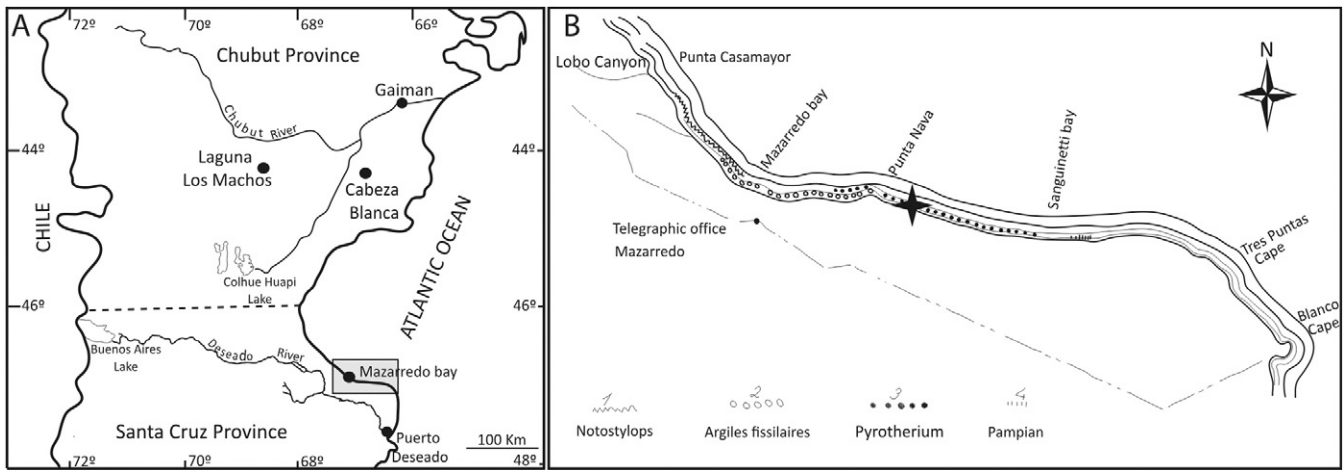
Patterson and Wood (1982) recognized Caviioidea sensu stricto (Caviioidea s.s.) clustering the extant and extinct Caviidae together with a diverse assemblage of extinct taxa grouped in the family Eocardiidae. Caviioidea s.s. shares unique dental and mandibular features such as the heart-shaped occlusal surface, hypsodonty, and reduced lateral deflection of the angular process. Recent phylogenetic analyses of this group based on morphological characters (Pérez and Vucetich, 2011a, 2011b) corroborated the monophyly of Caviioidea s.s., but retrieved a paraphyletic arrangement of “eocardiids” as successive sister taxa of the crown-group Caviidae.

The Caviioidea s.s. includes a large diversity of extinct species which were an important component of the vertebrate fauna during the Neogene (Vucetich and Verzi, 1995; Vucetich et al., 1999). Their fossil record begins in the Deseadan South American

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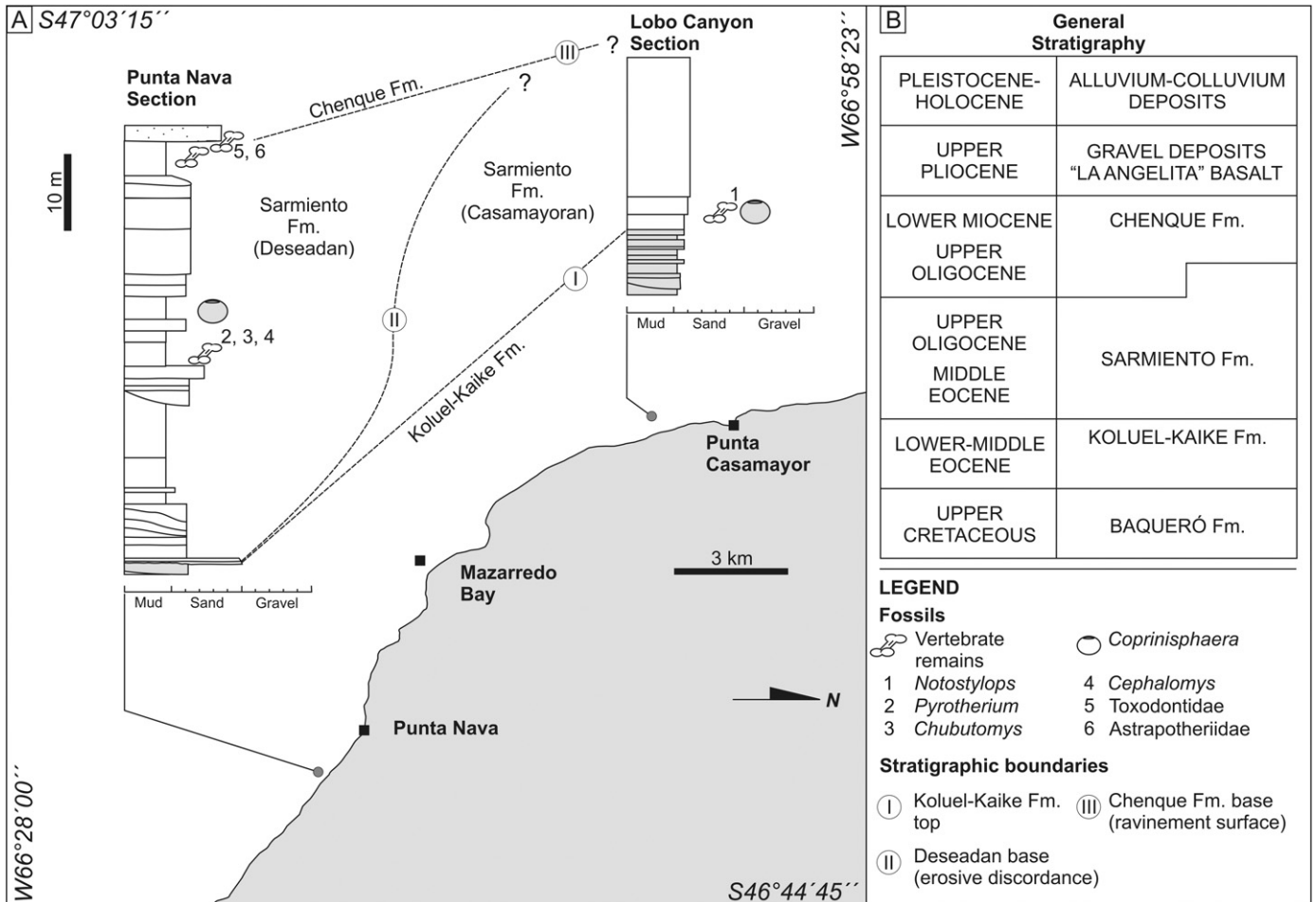


**Fig. 1.** Location map and stratigraphic profile. **A.** Principal Patagonian localities mentioned in the text. **B.** Detail of the study area modified from Ameghino (1906: fig. 25). The star indicates the studied locality.

Land Mammal Age (SALMA; late Oligocene). The temporal extension of the Deseadan is still controversial but encompasses a long period of at least five million years (24.5–29 Ma, Flynn and Swisher, 1995; Carlini et al., 2009). As the oldest representatives of the group, the Deseadan cavioids s.s. are relevant, although known through very scarce materials of only two species: *Asteromys punctus* Ameghino, 1897, from Cabeza Blanca and Laguna

Machos, Chubut Province, Argentina (Fig. 1; Pérez and Vucetich, 2012), and *Chubutomys simpsoni* Wood and Patterson, 1959, known only from Cabeza Blanca (Fig. 1). Therefore, new materials of Deseadan cavioids are of prime importance to understand the early evolution of this group.

Punta Nava is placed in northeastern Santa Cruz Province (Patagonia, Argentina; Figs. 1 and 2). This locality is known for its



**Fig. 2.** A. General sections at northern Santa Cruz Province including Paleogene mammal records and main stratigraphical relationships. B. General stratigraphy in the study area (based on Giacosa et al., 1998).

fossil mammal assemblage assigned to the Deseadan SALMA (e.g., *Pyrotherium*, *Leontinia*; Tornoüer, 1903; Ameghino, 1906), but no rodent remains were known so far. A recent fieldwork provided the first findings of fossil caviomorphs, including representatives of Cavoioidea, Octodontoidea, Chinchilloidea, and Erethizontoidea. Here we describe a new species of Cavoioidea s.s. from Punta Nava and we evaluate its phylogenetic affinities. This new cavioid from the Deseadan SALMA, and the reinterpretation of the tooth morphology of *Chubutomys simpsoni*, provide new insights into the early diversification of Cavoioidea s.s.

## 2. Geological setting

Punta Nava is located in the northeast of the Santa Cruz Province, Patagonia, Argentina (S 47° 02', W 69° 29'; Figs. 1 and 2). The study site is formed by a stratigraphic suite including the Koluel-Kaike (Lower–Middle Eocene), Sarmiento (Middle Eocene–Lower Miocene), and Chenque (Lower Oligocene–Lower Miocene) formations, all of them covered by Quaternary gravel deposits and showing lithologic features similar to those recognized in the Gran Barranca area (South Chubut Province) (Bellosi, 1995, 2010; Krause et al., 2010; Raigemborn et al., 2010). The fossil-bearing beds are the whitish tuffs of the Sarmiento Formation. This unit overlies in erosive discordance the silicified and pedogenized tuffs of the Koluel-Kaike Formation, and is covered, also in erosive discordance, by the marine deposits of the Chenque Formation. A preliminary sedimentary analysis of the Sarmiento Formation in the study site allowed recognizing facies of both floodplains and moderate to high sinuosity channels formed by tuffs and mudstones as dominant fractions with subordinate intraformational conglomerates. The material studied herein proceeds particularly from the finer facies (fine tuffs and mudstones).

## 3. Material and methods

Suprageneric taxon names are used as defined by Pérez and Vucetich (2011b). Cavoioidea includes Dasyproctidae, Cuniculidae, “Eocardiidae”, and Caviidae. The use of Cavoioidea sensu stricto encompasses “Eocardiidae” and Caviidae; “Eocardiidae” is paraphyletic; therefore, quotation marks are used for this assemblage of basal cavioids (Pérez, 2010; Pérez and Vucetich, 2011a, 2011b). The crown-group of Cavoioidea s.s. is formed by Caviidae (Caviinae, Dolichotinae, and Hydrochoerinae), excluding the basal forms of Cavoioidea s.s. (i.e., “eocardiids”). The dental nomenclature follows Candela (1999), Marivaux et al. (2004), and Pérez (2010). Mandibular nomenclature follows Pérez (2010), modified from Woods (1972) and Woods and Howland (1979).

**Institutional abbreviations:** AMNH: American Museum of Natural History, Division of Paleontology, New York; MPEF-PV: Museo Paleontológico “Egidio Feruglio”, Paleontología de Vertebrados, Trelew; MPM-PV: Museo Regional Padre Molina, Colección Paleontología de Vertebrados, Río Gallegos.

## 4. Results

### 4.1. Systematic Paleontology

Order RODENTIA Bowdich, 1821

Suborder HYSTRICOGNATHI Tullberg, 1899

Superfamily CAVIOIDEA Fischer de Waldheim, 1817

Genus *Chubutomys* Wood and Patterson, 1959

**Type species:** *Chubutomys simpsoni* Wood and Patterson, 1959.

**Occurrence:** Sarmiento Formation, Chubut and Santa Cruz Provinces, Argentina; Deseadan SALMA (late Oligocene). The generic assignment of the recently described Colhuehuapian

species *Chubutomys leucoreios* Pérez et al. (2010) is questioned in this contribution (see Discussion).

**Emended diagnosis:** *Chubutomys* is diagnosed by the following unique combination of characters (synapomorphies marked with an asterisk): protohypodont cheek teeth; bilobed molars; lingual wall in lower teeth straight and lacking a longitudinal furrow\* (reversal to the condition present in *A. punctus* and more basal forms than Cavoioidea s.s.); absence of mesofossetid already in young-adult ontogenetic stages (shared with “*Chubutomys*” *leucoreios* and with *Phanomys* + euhyposodont cavioids); hypoflexid extending transversely more than half of the crown, with cement; lateral crest curved and deflected anteroventrally from the base of the coronoid process. *Chubutomys* differs from *Eocardia*, *Schistomys*, *Matiamys*, *Microcardiodon*, *Guiomys*, and Caviidae in having rooted cheek teeth.

*Chubutomys simpsoni* Wood and Patterson, 1959

Fig. 3

**Holotype:** AMNH 29557 left mandibular fragment with m1–m2.

**Occurrence:** Cabeza Blanca, Escalante Department, Chubut Province, Argentina (Fig. 1(A)). Sarmiento Formation, Deseadan SALMA (late Oligocene).

**Emended diagnosis:** Cavioid diagnosed by the following unique combination of characters: enamel interrupted at the base of the lingual wall, posterolingual corner, and on anterior surface; funnel-shaped hypoflexid in occlusal view (narrow in the lingual end, widening towards the labial side); m1–m2 formed by triangular lobes, with convex anterior and posterior walls, and lingual pit of each lobe well marked (in occlusal view); lingual end of the hypoflexid not extending beyond the labial ends of the internal fossetids.

**Remarks:** *Chubutomys simpsoni* was described by Wood and Patterson (1959) on the basis of a single specimen, a mandibular fragment with m1–m2 (holotype AMNH 29557). The presence of cement in *C. simpsoni* was previously overlooked (Wood and Patterson, 1959; Kramarz, 2006; Pérez et al., 2010) because the cement is only preserved in the bottom of the hypoflexid and up to little more than half of the crown height, and is only visible under high magnification. This region is partly covered with sediment and remains of latex but the cement is distinctly colored and can be distinguished under binocular scope (Fig. 3(E)).

*Chubutomys navaensis* nov. sp.

Fig. 4

**Derivation of name:** In reference to the type-locality name, Punta Nava.

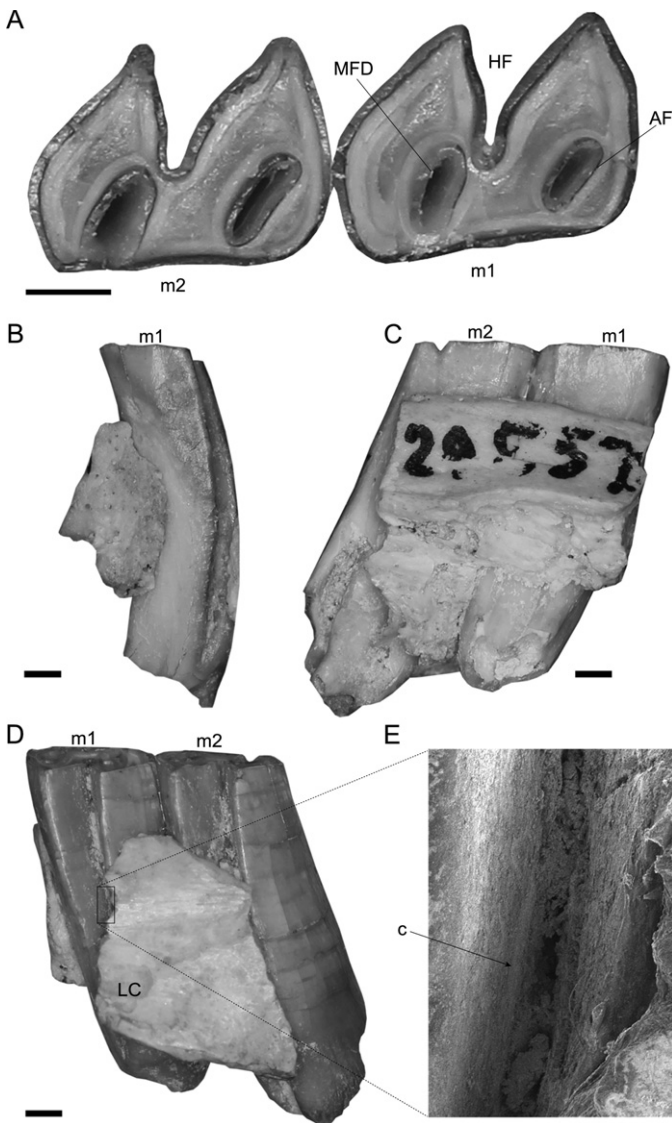
**Holotype:** MPM-PV 4877, right mandibular fragment with base of incisor and moderately worn p4–m3.

**Referred material:** MPM-PV 4878, isolated left m2.

**Occurrence:** Punta Nava, northeastern Santa Cruz Province (Fig. 1). Sarmiento Formation, Deseadan SALMA (late Oligocene).

**Diagnosis:** Cavioid diagnosed by the following unique combination of characters (autapomorphies marked with an asterisk): anterior wall straight and posterior one gently convex in each lobe of the p4–m1\*; notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* located at the level of the m1 and m2\*, and connected to the masseteric crest; mandibular foramen probably posterior to m3\*; mental foramen dorsolaterally oriented; projection of the posterior end of the mandibular symphysis moderately developed; alveolar protuberance absent. Differs from *Chubutomys simpsoni* and “*Chubutomys*” *leucoreios* in having a longer and narrower hypoflexid, an interruption of the enamel at the base and the corner of the lingual wall of the crown, cheek teeth having lower crowns, and in having more rounded fossetids. Differs from “*Chubutomys*” *leucoreios* in displaying cement in the hypoflexid, and a p4 lacking a mesofossetid since the young-adult ontogenetic stage.





**Fig. 3.** *Chubutomys simpsoni* holotype AMNH 29557, left m1–2. **A.** Occlusal view. **B.** Anterior view. **C.** Labial view. **D.** Lingual view. **E.** Detail of cement. Abbreviations: AF: anterofossetid; C: cement; HF: hypoflexid; LC: lateral crest; MFD: metafossetid. Scale bars: 1 mm.

**Description:** *Chubutomys navaensis* nov. sp. is a small basal cavioid s.s., similar in size to *A. punctus* and *Chubutomys simpsoni* (Fig. 3(A–D); Table 1). The hemimandible is well preserved, but lacks its anterior and posterior portions (Fig. 4(A, B)). In labial view, the mental foramen is close to the dorsal margin of the diastema and opens dorsolaterally (Fig. 4(A)), as in other stem Caviioidea s.s. (e.g., *A. punctus*, “*C.*” *leucoreios*, *Luantus propheticus*, *Eocardia excavata*, *Schistomys erro*, *Guiomys unica*). The posteroventral projection of the posterior end of the mandibular symphysis is moderately developed, having only a low bulge that projects ventrally and is marginally exposed in lateral view, as in *A. punctus*, “*C.*” *leucoreios* or *L. propheticus*. The lateral crest is curved and deflects anteroventrally from the base of the coronoid process, resembling the condition of all stem cavioids. The notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* (nMpi) is located at the level of the m1 and m2 and is connected to the masseteric crest, thereby forming a well-developed ridge that fails to project laterally with respect to the lateral surface of the dentary. Only the anterior portion of the horizontal crest is preserved, and appears as a wide and low ridge (Fig. 4(A)).

**Table 1**

Dental measurement of *Chubutomys navaensis* nov. sp. and *Chubutomys simpsoni* (in mm).

	APL	AW	PW	hH
<i>Chubutomys navaensis</i> nov. sp.				
MPM-PV 4477 (Holotype)				
p4	2.95	1.7	2.32	
m1	2.61	2.2	2.54	
m2	2.82	2.72	2.78	
m3	3.00	2.63	2.24	
i	1.44	1.95		
MPM-PV 4478				
m2	2.82	1.98	2.33	5.43
<i>Chubutomys simpsoni</i>				
AMNH 29557 (Holotype)				
m1	3.3	2.5	2.6	6.8
m2	3.5	2.6	2.5	

APL: anteroposterior length; AW: anterior width; PW: posterior width; hH: hypoflexid height.

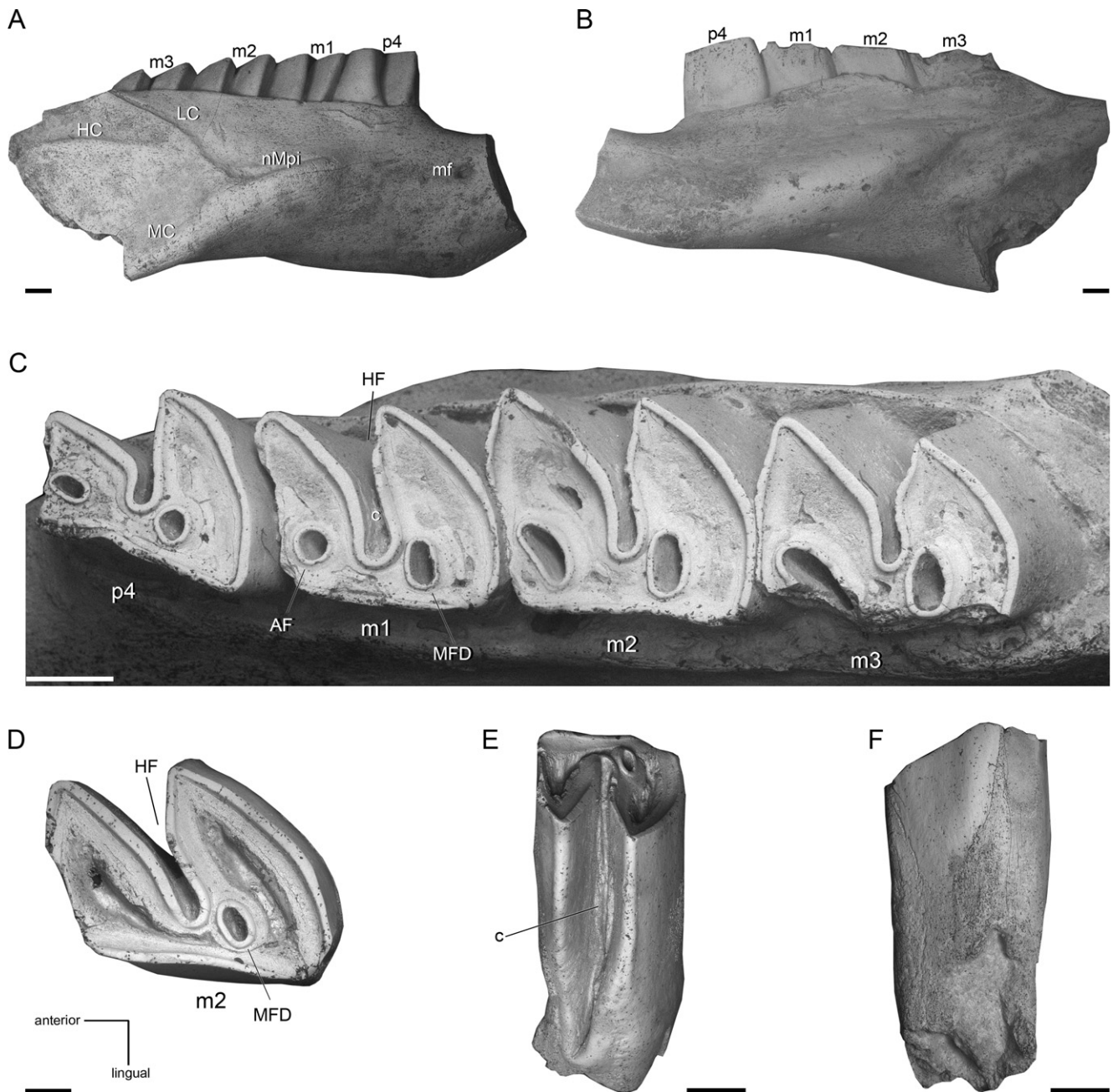
*Chubutomys navaensis* nov. sp. lacks the alveolar protuberances as in *A. punctus* and “*C.*” *leucoreios*. *Chubutomys navaensis* nov. sp. lacks a mandibular foramen in the preserved portion of the dentary (Fig. 4(B)), differing from the condition in all known Caviioidea s.s. with relatively complete jaw fragments, which have this foramen below the m3. However, it must be noted that *C. simpsoni*, *Luantus initialis*, *L. minor*, *L. toldensis*, *Phanomys mixtus*, *P. vetulus*, and some euhypsodont cavioids are known only by fragmentary mandibular remains, and therefore the position of the mandibular foramen cannot be determined.

The incisor is broken slightly in front of the level of the mental foramen. It is slender and triangular in cross-section. In lingual view, the incisor extends up to the level of the posterior part of the m2 (inferred from its alveolus; Fig. 4(B)), as in *A. punctus*.

The cheek teeth of *Chubutomys navaensis* nov. sp. are protohypsodont and bilobed (Fig. 4(C)). The enamel is interrupted, forming dentine tracks at the anterior and posterior lingual corners, from the base but not reaching the occlusal surface in juveniles. These dentine tracks are triangular in shape (Fig. 4(F)) and thus, the area without enamel at the occlusal surface enlarges with wear. The enamel is also interrupted at the anterior face of m1 and m2 (Fig. 4(C–D, F)). The teeth have cement in the hypoflexid, in contrast to the condition of the most basal forms of Caviioidea s.s. (i.e., *A. punctus*, *L. initialis*, *L. minor* and “*C.*” *leucoreios*). The cement is distributed from base of hypoflexid up to three quarters of its height, and is more abundant than in *C. simpsoni*. The presence of cement is recorded in more derived taxa, such as *C. simpsoni* (Fig. 3(E)), *L. propheticus*, *L. toldensis*, *P. mixtus*, *P. vetulus* and all euhypsodont cavioids.

The p4 (Fig. 4(C); Table 1) is smaller than molars, and its lobes differ in size and shape, as in “*C.*” *leucoreios* and *L. propheticus*. The anterior lobe is smaller than the posterior one, and is sub-quadrangular in cross-section, with a straight anterior wall and a convex postero-labial wall. The posterior lobe is transversely wider than the anterior one, with a convex posterior wall and a straight anterior margin. The premolar has antero- and metafossetid, but lacks a mesofossetid (at least in the young-adult ontogenetic stage of this specimen). This condition is different from p4 of all other protohypsodont taxa of the stem Caviioidea s.s., which have a mesofossetid in young-adult ontogenetic stages (e.g., *A. punctus*, “*C.*” *leucoreios*, *L. propheticus*, and *P. mixtus*). However, the p4 of *L. minor* and *C. simpsoni* are unknown. In labial view, the hypoflexid is close to the level of the alveolar line (Fig. 4(A)).

The p4–m1 length is shorter than m2–m3 (Fig. 4(C)); (Table 1), as in most species of the stem group of Caviioidea s.s. and some Caviidae (e.g., *Microcavia*, *Hydrochoerus*). The molars show some little holes in the occlusal surface corresponding to breakages in the dentine, not to fossetids (Fig. 4(C)).



**Fig. 4.** *Chubutomys navaensis* nov. sp. **A–C**, MPM-PV 4477, holotype, right mandible; **D–F**, MPM-PV 4478, left m2. **A, E**. Labial view; **B, F**. Lingual view; **C, D** (reversed): occlusal view. Abbreviations: AF: anterofossetid; C: cement; HC: horizontal crest; HF: hypoflexid; LC: lateral crest; mf: mentonian foramen; MFD: metafossetid; m1–m3: lower molars; nMpi: notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*. Scale bars: 1 mm.

In occlusal view, the m1–m3 (Fig. 4(C)) are bilobed, and the base of each lobe is broad; the lingual wall is straight, resembling the condition of *C. simpsoni*. At this stage of wear the anterior lobe is mesiodistally narrower than the posterior one in m1, subequal in m2, and wider in m3. The anterior wall of each lobe in m1–m2 is nearly straight but the posterior wall is convex. The hypoflexid is narrow, extremely long, and extends beyond the transverse midpoint of the crown, differing from “*C.* leucoreios in which the hypoflexid is triangular and extends only up to the transverse midpoint of the crown, and from *C. simpsoni* in which the hypoflexid is slightly funnel-shaped (Fig. 3(A)). The molars are similar in size, but m2 is larger than m1 and m3. All teeth have antero- and metafossetids, but lack mesofossetid (as in *C. simpsoni* and “*C.* leucoreios). The anterofossetid of m1 is subcircular and the

metafossetid is transversally elongated. The anterofossetid of m2–m3 is obliquely elongated, and the metafossetid is transversally elongated; the fossetids are larger than those of p4 and m1. The left isolated m2 MPM-PV 4878 (Fig. 4(D–F)) shows a similar morphology as the m2 of the holotype, but in a later stage of wear, and has only the metafossetid. The lobes in this specimen are more oblique and the anterior lobe is transversally shorter. In *C. simpsoni* (Fig. 3(A–D)) and “*C.* leucoreios the fossetids are narrower and more elongated than in *Chubutomys navaensis* nov. sp. However, these differences could be the result of different ontogenetic stages. In the m2 of the holotype of *C. simpsoni*, and the p4 and m3 of the holotype of “*C.* leucoreios, the metafossetid are still open on the lingual side, suggesting a less advanced stage of wear than in the holotype of *C. navaensis* nov. sp.



#### 4.2. Phylogenetic analysis

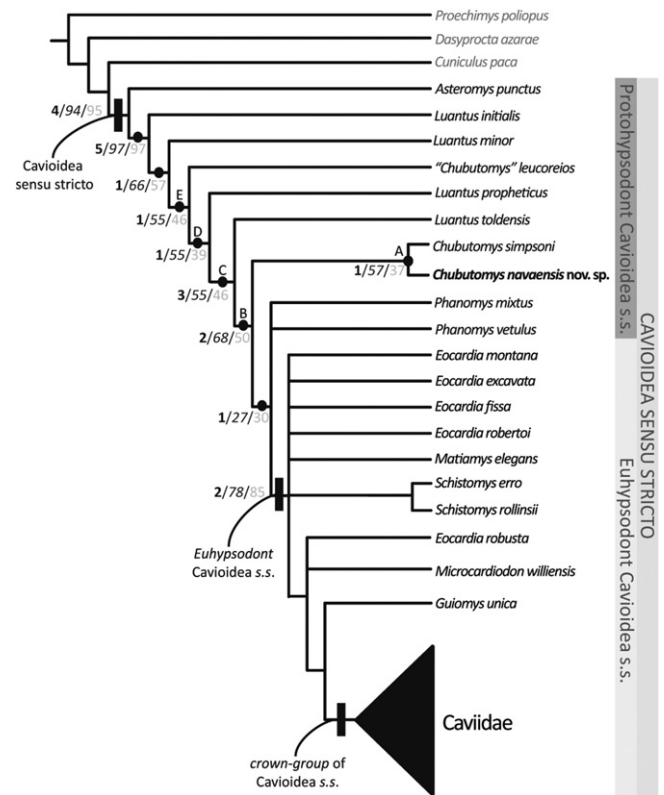
The phylogenetic relationships of *Chubutomys navaensis* nov. sp. were assessed using a modified version of the dataset of Pérez and Vucetich (2012), which includes 41 cavioids scored for 95 morphological characters and DNA sequences of four genes (*12S*, *Cytb*, *GHR*, and *TTH*) for eight extant cavioids (Appendix A, Supplementary material). *Chubutomys navaensis* nov. sp. was scored for the morphological characters (Appendix B, Supplementary material) and included in the concatenated dataset of morphology and DNA data. Some multistate characters of the morphological partition were considered as additive based on increasing degrees of similarity between the character states or in cases of interested homologies. This dataset contained a total of 41 taxa and 4.303 characters (Appendix C, Supplementary material). Some representatives of Caviioidea were used as outgroup taxa: *Dasyprocta azarae*, *Neoreomys australis* (Dasyproctidae), and *Cuniculus paca* (Cuniculidae). The phylogenetic trees were rooted with an octodontoid caviomorph, *Proechimys poliopus*.

This dataset was analyzed (Appendix D, Supplementary material) using equally weighted parsimony in TNT 1.1 (Goloboff et al., 2008a, 2008b), treating gaps as missing data for DNA sequences. We use equally weighted parsimony to minimize the number of postulated evolutionary transformations. The heuristic search consisted of 1000 replicates of Wagner trees with random addition sequence of taxa, followed by TBR branch swapping, collapsing zero-length branches under the strictest criterion. After this procedure, a final round of TBR branch swapping was applied to find all most parsimonious trees (MPTs). Support values were calculated using Bremer indices, Bootstrap, and Jackknife, and several constrained searches were run to test alternative placements of *Chubutomys* and related species.

The parsimony analysis resulted in a total of 48 trees of 3166 steps (CI = 0.644; RI = 0.481). The strict consensus is shown in Fig. 5. The phylogenetic analysis was also performed only with the morphological characters, and resulted in 36 most parsimonious trees of 316 steps. The topology of the stem group of Caviioidea s.s. is exactly the same in both analyses. Hence, only the results based on the total evidence are shown here. All the most parsimonious hypotheses of this analysis placed *Chubutomys navaensis* nov. sp. forming a monophyletic group with *Chubutomys simpsoni* (Fig. 5, node A). The only unambiguous synapomorphy that supports this clade is the absence of a longitudinal furrow on the lingual wall (character 34[0]). This clade is the sister group of *Phanomys mixtus* + *Phanomys vetulus* + euhypsodont cavioids (Fig. 5, node B), and is supported by two unambiguous synapomorphies: hypoflexid narrow and transversally long in occlusal view (character 33[2]), and absence of mesofossetid in young-adult ontogenetic stages (character 52[1]).

Several species of the paraphyletic genus *Luantus* are successive sister taxa of the clade formed by *Chubutomys*, *Phanomys*, and euhypsodont cavioids. The node of *Luantus toldensis* and more derived cavioids (Fig. 5, node C) is supported by three unambiguous synapomorphies: hypoflexid extending beyond the transverse midpoint of the crown, in occlusal view (character 32[2]); presence of cement in juvenile ontogenetic stages (character 44[1]); absence of fossetids in late ontogenetic stages (character 47[1]). The node formed by *Luantus propheticus* and more derived cavioids (Fig. 5, node D) is supported by a single unambiguous synapomorphy: presence of cement in young-adult ontogenetic stages (character 43[1]).

*Chubutomys leucoreios* is depicted basally to all these forms (Fig. 5, node E), as it has the plesiomorphic condition for all the above-mentioned characters, thereby rejecting its current generic assignment (see next Section). The node formed by this taxon and



**Fig. 5.** Strict consensus of the 48 most parsimonious trees (Length = 3166; CI = 0.644; RI = 0.481) resulting from cladistic analysis of a modified matrix of Pérez and Vucetich (2012; Appendix C, Supplementary material). *Chubutomys navaensis* nov. sp. and *Chubutomys simpsoni*, form a monophyletic group (node A), and this clade is the sister group of the node formed by *Phanomys mixtus*, *Phanomys vetulus* and euhypsodont Caviioidea s.s. (node B). The letters indicate the node, numbers in bold indicate Bremer indices, numbers in italic represent absolute/GC Jackknife values, and numbers in gray represent absolute/GC Bootstrap values.

more derived cavioids is supported by the presence of a longitudinal furrow on the lingual wall (character 34[1]).

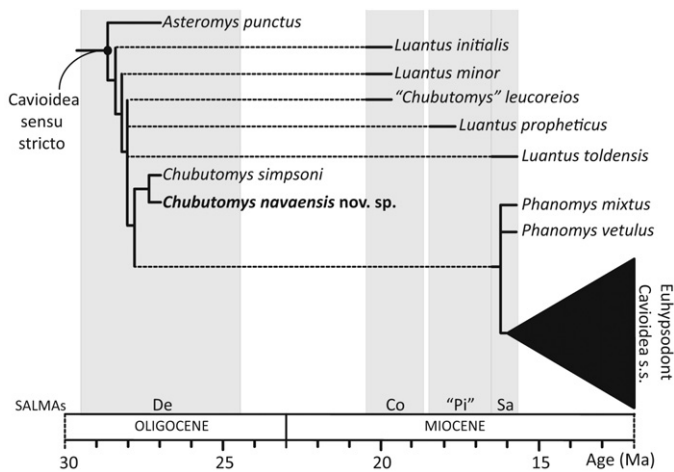
## 5. Discussion

### 5.1. Affinities of *Chubutomys*

The phylogenetic analysis corroborates the monophyly of a group formed by *Chubutomys navaensis* nov. sp. and *Chubutomys simpsoni* (Fig. 5, node A, and Fig. 6), which is placed as one of the most derived lineages of protolysodont cavioids (being only more basal than *Phanomys*). These phylogenetic results contrast with previous interpretations on the affinities of *Chubutomys* and have important implications both for taxonomic purposes and for understanding the evolution of Caviioidea s.s.

Traditionally, *Chubutomys* has been interpreted as belonging to a different lineage from *Asteromys-Luantus* (Wood and Patterson, 1959), and as one of the most basal species of Caviioidea s.s. (Kramarz, 2006). Recent phylogenetic analyses of this group (Pérez and Vucetich, 2011a, 2011b) also placed *Chubutomys simpsoni* basally within Caviioidea, as closely related to *Chubutomys leucoreios* and basal to *Luantus propheticus* and *L. toldensis*.

Our results rely on the new information provided by *Chubutomys navaensis* nov. sp. and from a revision of the holotype of *C. simpsoni*. In particular, Wood and Patterson (1959) interpreted that *C. simpsoni* lacks cement in its cheek teeth, which has been regarded as a diagnostic character of this taxon. However, both the holotype of *Chubutomys simpsoni* and *Chubutomys navaensis* nov.



**Fig. 6.** Stratigraphically calibrated strict consensus, showing the position of *Chubutomys navaensis* nov. sp and *C. simpsoni* and the ghost lineages of protohypsodont Caviioidea sensu stricto. In dashed line, six ghost lineages from the Deseadan radiation. Abbreviations: Co: Colhuehuapian; Ma: Million years ago; "Pi": Pinturan; SALMA: South American Land Mammals Age; Sa: Santacrucian. SALMAS temporal extension based on Flynn and Swisher (1995), Kramarz and Bellosi (2005), and Ré et al. (2010).

sp. have cement in the hypoflexid, at least from the base to close to the apex of the crown (Figs. 3 and 4). The presence of cement in young-adult ontogenetic stage is one of the features that place *C. simpsoni* in a higher position in the phylogeny of this group in comparison with previous hypotheses.

The new phylogenetic results separate the clade formed by *Chubutomys simpsoni* and *Chubutomys navaensis* nov. sp. from "*Chubutomys*" *leucoreios* (Bryn Gwyn, Chubut Province, Fig. 1; Colhuehuapian SALMA, early Miocene; Flynn and Swisher, 1995), challenging the generic assignment of the latter taxon. "*Chubutomys*" *leucoreios* exhibits a set of plesiomorphic characters (e.g., absence of cement, hypoflexid V-shaped in occlusal view, enamel continuous) that place it well nested within the most basal cavioids s.s., traditionally referred to the genus *Luantus*, which appears paraphyletic. These results indicate that the taxonomy and generic assignment of all these protohypsodont cavioids need to be revised. For the moment, we have opted to avoid the erection of new genera for these taxa given that the character support for this area of the phylogenetic tree is relatively low. Further studies based on more complete materials are necessary to achieve robust phylogenetic results upon which a solid taxonomy should be constructed.

## 5.2. Evolutionary implications

The results of this analysis have important evolutionary implications for understanding the radiation of basal cavioids s.s. As mentioned above, only a few specimens of Caviioidea s.s. were previously known from the Deseadan SALMA: two mandibular fragments of *A. punctus* and the fragmentary holotype of *Chubutomys simpsoni*. The new remains consisting of a mandibular fragment and an isolated tooth of *Chubutomys navaensis* nov. sp. increase the knowledge of this group during the Deseadan SALMA (Fig. 6). Despite this low diversity and abundance, the morphological and phylogenetic information provided by these species is critical for understanding the early evolutionary history of this group. In the present phylogenetic analysis, *Chubutomys simpsoni* and *Chubutomys navaensis* nov. sp. (from the late Oligocene) are placed in a higher position than in previous analyses (Pérez and Vucetich, 2012), being the sister group of *Phanomys* and euhypsodont cavioids. The higher position of the Deseadan

*Chubutomys* creates multiple ghost lineages leading to all the species of *Luantus* and a long ghost lineage for the *Phanomys* + euhypsodont Caviioidea s.s. that must have originated during the Deseadan SALMA or even earlier (Fig. 6). Therefore, all protohypsodont lineages would have originated in an early radiation of this group. The extensive ghost lineages and the poor record of Caviioidea s.s. during the Deseadan SALMA in high latitudes of South America (i.e., Patagonia, Argentina), and its absence in middle and low latitudes (e.g., Salla, Lacayani, in Bolivia; Moquegua in Peru) could be explained by the incompleteness of the sedimentary record (e.g., non-depositional hiatuses), and by the geographic sampling of the rodent fossil record across South America, that is clearly biased towards fossils found at higher latitudes. In addition, Carlini et al. (2009) suggest that the Deseadan as traditionally conceived actually, could encompass a large amount of time. If this is true, then the early evolution of Caviioidea s.s. during this time could have been longer than previously proposed.

The branch support values for various nodes within the stem of Caviioidea s.s. are moderate, with Bremer support values ranging between 1 and 3, jackknife frequencies ranging between 68 and 98, and bootstrap frequencies ranging between 46 and 95 (Fig. 5). The relatively low values in nodes of basal protohypsodont cavioids are caused by the unstable behavior of several of these taxa that are represented by incomplete specimens (e.g., *Luantus minor*, "*Chubutomys*" *leucoreios*, *Luantus propheticus*). However, the only alternative phylogenetic hypotheses that would reject the inferred radiation of protohypsodont cavioids during the Deseadan SALMA would be those that place *Chubutomys* next to *Asteromys*, at the base of Caviioidea s.s. When *Chubutomys* is forced to be placed close to *Asteromys*, four extra steps are required in our phylogenetic dataset. Therefore, these results reveal a higher phylogenetic position of *Chubutomys*, and provide phylogenetic evidence for a rapid early diversification of cavioids s.s., which was more extensive than previously thought.

## 6. Conclusions

*Chubutomys navaensis* nov. sp. is part of the stem group of Caviioidea s.s. It is described here evaluating its phylogenetic relationships and evolutionary implications. The new species comes from the late Oligocene (Deseadan SALMA) of Punta Nava (Patagonia, Argentina), being the first record of a cavioid rodent from this locality. *Chubutomys navaensis* nov. sp. forms a monophyletic group together with *Chubutomys simpsoni*, and this clade is depicted as the sister group of *Phanomys* and more derived cavioids.

The revision of the holotype of *Chubutomys simpsoni* showed the presence of cement in the hypoflexid of this young-adult specimen. This leads to place *C. simpsoni* in a higher phylogenetic position than in previous studies (Wood and Patterson, 1959; Kramarz, 2006; Pérez, 2010; Pérez and Vucetich, 2011a, 2011b). "*Chubutomys*" *leucoreios* is placed more basally than *Chubutomys navaensis* nov. sp. + *C. simpsoni*, nested within the species of the genus *Luantus*, which appears paraphyletic, thereby implying that "*C.*" *leucoreios* should be assigned to another genus. Finally, the record of *Chubutomys navaensis* nov. sp. in the late Oligocene, and the higher position of *Chubutomys* in the cavioid phylogeny, imply that the origin of all protohypsodont lineages of Caviioidea s.s. took place during the Deseadan SALMA. In this way, the early evolution in Caviioidea s.s. would have occurred through a major diversification pulse, larger than previously proposed.

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#### Appendices A–D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.geobios.2012.06.001>.

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