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A new species of the tetraploid vizcacha rat *Tympanoctomys* (Caviomorpha, Octodontidae) from central Patagonia, Argentina

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A new living species of the desert-adapted tetraploid rodent *Tympanoctomys* (Caviomorpha, Octodontidae) is described. The new form is restricted to the type locality in Chubut Province, central Patagonia, Argentina, although is known from at least 4 additional Holocene-aged localities along the middle and lower valley of the Chubut River. *Tympanoctomys* sp. nov. is smaller than the living *T. barrerae*, its general coloration is yellowish (reddish in *T. barrerae*) and its tail is equal to ~43–50% of head and body length (~49–53% in *T. barrerae*). Its skull and dentition are characterized by a unique combination of morphological traits, including narrow and posteriorly acuminate nasals (broad and barrel-shaped in *T. barrerae*), supraoccipital not laterally expanded (expanded in *T. barrerae*), and 8-shaped lower 3rd molar (comma-shaped in *T. barrerae* and †*T. cordubensis*). Morphometric and genetic evidence supports the specific distinction of this Patagonian endemic *Tympanoctomys*, also characterized by smaller sperm than *T. barrerae*. The reduced range of the new species, coupled with its recent extinction from the Chubut River valley and the potential impact of large uranium mining projects in central Patagonia, suggest that this species faces a severe extinction risk in the short term.

Key words: *Pipanaoctomys*, *Salinoctomys*, octodontids, taxonomy, Chubut

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The family Octodontidae is a moderately rich group (~13 species) of South American caviomorph rodents; however, from an ecological viewpoint, this is a diverse clade including cursorial to scansorial and epigeous to strictly subterranean forms (Gallardo et al. 2007; Ojeda et al. 2012; Upham and Patterson 2012). These rodents are mostly restricted to the western portion of southern South America, between 15°S and 43°S, on both sides of the Andes (Reig 1986, 1989; Ojeda et al. 1996, 2012; Mares et al. 2000; Gallardo et al. 2007). Octodontids occupy a variety of habitats, from humid environments that are shrubby or forested (*Aconaemys*, *Octodon*, and *Spalacopus*), to bare rocky outcrops (*Octodontomys*), deserts, and saline basins (*Octomys*, *Pipanaoctomys*, *Salinoctomys*, and *Tympanoctomys*).

The living octodontid radiation is usually linked with the uplift of the Andes during the late Miocene, a geologic process that partially triggered the formation of large deserts and open areas (Contreras et al. 1987; Verzi et al., in press). Octodontid species that live east of the Andes are mainly adapted to xeric environments, including extreme habitats such as salt flats and basins (Gallardo et al. 2007). Some of these taxa, such as the genera *Tympanoctomys*, *Pipanaoctomys*, and *Salinoctomys*,

have remarkable ecomorphological adaptations for life in xeric habitats, including well-inflated auditory bullae, unusual capacity to concentrate urine through a specialized kidney, and a rigid bundle of buccal hairs to remove the salt excess from chenopod leaves (e.g., Ojeda et al. 1996, 1999; Mares et al. 1997; Diaz and Ojeda 1999; Diaz et al. 2000; Berman 2003).

The genus *Tympanoctomys* includes 2 species, the living *T. barrerae* and the fossil *T. cordubensis* (Woods and Kilpatrick 2005). The 1st is endemic to arid to semiarid regions of central-western Argentina (Diaz et al. 2000; Ojeda 2010), whereas the 2nd had been reported from Pleistocene deposits (0.90–0.78 million years ago [mya]) of central and central-eastern Argentina (Verzi et al. 2002). *Tympanoctomys* is unique among desert mammals, not only by its set of morphological adaptations but also for its cytogenetic features. In fact, it has been corroborated to be tetraploid (Gallardo et al. 2006; Suárez-Villota et al. 2012) in spite of previous allegations (Svartman et al. 2005).





FIG. 1.—Holotype of *Tympanoctomys kirchnerorum*, n. sp., from central Chubut Province, Argentina (CNP 1862): external appearance of the animal photographed in the field camp.

The 1st report of *Tympanoctomys* sp. nov. in central Patagonia was made by Udrizar Sauthier et al. (2009) based on late Holocene remains. A living population was discovered almost at the same time and was referred to *T. barrerae* (Gallardo et al. 2009). However, phylogenetic and phylogeographic analyses of mitochondrial markers show that central Patagonian animals are highly divergent from those in central-western Argentina (Gallardo et al. 2013). In this paper we describe as a new species the population from central Chubut, Argentina, based on morphology and the available genetic data. This new form not only increases our knowledge about the diversity of the genus but also significantly expands the biogeographic significance of the Patagonian region in the octodontid family.

MATERIALS AND METHODS

Studied specimens.—The description of the new species of *Tympanoctomys* is based on livetrapped individuals and fossil remains recovered from Holocene deposits. Animals were collected from their burrows using Oneida-Victor # 0 traps (Oneida-Victor Inc., Ltd., Euclid, Ohio) protected with a rubber band to avoid individual damage following the procedures of the American Society of Mammalogists (Sikes et al. 2011), measured and weighed in the field, and prepared as skins and skeletons. Sperm, blood, and tissue samples also were secured. Fossils were obtained from caves and rock-shelters from stratigraphical deposits originated by the trophic activity of owls (Udrizar Sauthier et al. 2009; Pardiñas et al. 2012). All these specimens are housed in the Colección de Mamíferos del Centro Nacional Patagónico (CNP) and in the Colección de Material de Egagrópilas y Afines “Elio Massoia,” Centro Nacional Patagónico (CNP-E), both in Puerto Madryn, Chubut Province, Argentina. Additional specimens of octodontids used for comparisons are listed in Appendix I.

Morphological analysis.—Anatomical descriptions follow De Santis et al. (1991), Mares et al. (2000), and Verzi et al. (2002). Dental nomenclature follows Reig (1977) and Reig and

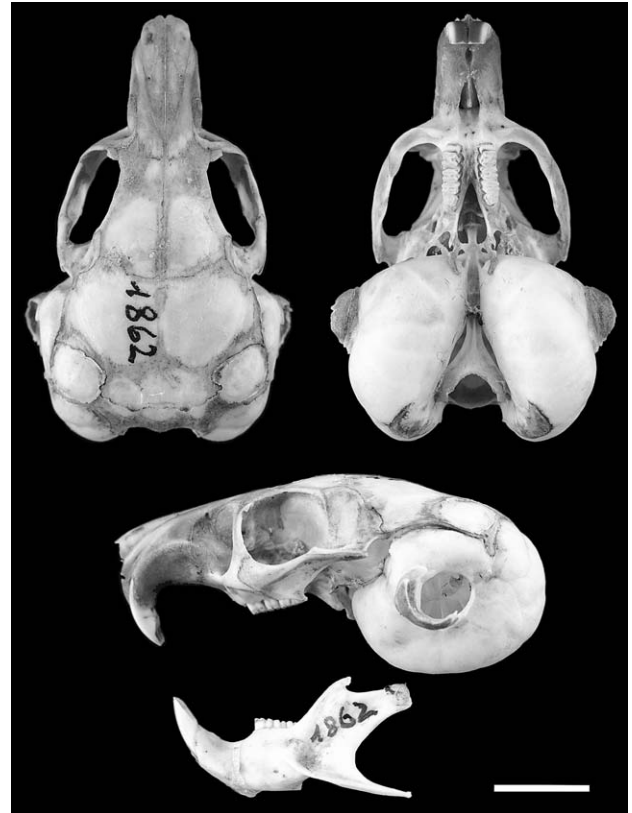


FIG. 2.—Holotype of *Tympanoctomys kirchnerorum*, n. sp., from central Chubut Province, Argentina (CNP 1862): skull in dorsal (top, left), ventral (top, right), and lateral (bottom) views, and left dentary in labial view. Scale = 5 mm.

Quintana (1991). Standard external measurements (in mm) were obtained from labels and field catalogs: total length, length of tail, length of hind foot, length of ear, and weight (in g). Twenty craniodental measurements were taken to the nearest 0.01 mm using a digital caliper. These are condylobasal length, rostral width, zygomatic breadth, interorbital breadth, nasal length, nasal width, frontal length, width of the inferior root of the zygomatic arch, upper diastema length, incise foramen length, incise foramen width, upper toothrow length, tympanic bullae length, tympanic bullae width, mastoid breadth, foramen magnum width, foramen magnum height, skull case height from the tympanic bullae, mandible length, and lower toothrow length. A principal component analysis was performed on a set of 23 adult specimens; principal components were extracted from a variance-covariance matrix and computed using the craniodental variables after transformation to their natural logarithms. These operations were made using the software Statistica (StatSoft, Inc. 2001). The new species of *Tympanoctomys* described here was primarily compared against *T. barrerae* and †*T. cordubensis* (Verzi et al. 2002). Because Díaz and Verzi (2006) claimed that the genera *Salinoctomys* and *Pipanoctomys* are junior synonyms of *Tympanoctomys*, a plausible hypothesis not fully documented (Gallardo et al. 2007), we also conducted a more reduced set of comparisons among those taxa. Finally,

the fossil form *Abalosia castellanosi*, retrieved as sister to *Tympanoctomys* (Reig and Quintana 1991; Verzi 2001; Verzi et al., in press), was briefly addressed to check potential similarities with the new Patagonian species.

RESULTS

FAMILY OCTODONTIDAE WATERHOUSE, 1839

Genus *Tympanoctomys* Yepes, 1942

Tympanoctomys kirchnerorum, sp. nov.

Figs. 1 and 2

Synonymy.—*Tympanoctomys barrerae*: Udrizar Sauthier et al. 2009:203; Gallardo et al. 2009:158 (part); Ojeda 2010:303 (part); Ojeda et al. 2012:290 (part); Pardiñas et al. 2012:72; Gallardo et al. 2013:454 (part).

Holotype.—CNP 1862 (Figs. 1 and 2), an adult male preserved as skin, partial skeleton, and tissues, collected on 18 March 2008 by M. H. Gallardo (field number MHG 1800).

Type locality.—Argentina, Province of Chubut, Department of Gastre, 18 km NNE by road of Los Adobes, conjunction between Ruta Provincial 58 and Zanjón El Colorado (43°13'51.6"S, 68°38'49.1"W, 517 m), according to the Topographic Chart, Instituto Geográfico Nacional, Buenos Aires, Argentina, Sheet 4369-IV, 1987, scale 1:250,000, called "Los Altares" (Fig. 3A, locality 1). This locality was recorded as "Estancia La Porfía (43°13'51.6"S, 68°38'49.1"W, 517 masl ...) approximately 20 km NE of Los Adobes, on provincial route 58" by Gallardo et al. (2009:158).

Paratypes.—Eight specimens collected at the type locality, as follows: CNP 2387, adult female, preserved as skin, skull, mandible, and partial skeleton (field number MHG 1799); CNP 2503, young female, flat skin, skull, mandible, and partial skeleton (MHG 1821); CNP 2504, adult female, flat skin, skull, mandible, and partial skeleton (MHG 1822); CNP 2505, adult female, flat skin, skull, mandible, and partial skeleton (MHG 1817); CNP 2386, adult male, skin, skull, mandible, and partial skeleton (MHG 1802); CNP 2501, young male, flat skin, skull with broken frontals, parietals, and occipital, mandible, and partial skeleton (MHG 1820); CNP 2502, young male, flat skin, broken skull, mandible, and partial skeleton (MHG 1819); and CNP 3632, adult male, skinned specimen in fluid (MHG 1818).

Additional material.—CNP-E 333, right dentary from a fresh owl pellet, 3 km W of type locality (43°13'50"S, 68°40'59"W, Province of Chubut, Argentina).

Assigned fossil materials.—All the following remains are late Holocene in age and were recovered from paleontological sites along the middle and lower course of the Chubut River, Chubut, Argentina (Udrizar Sauthier et al. 2009; Pardiñas et al. 2012): Los Altares Profile (43°53'35", 68°23'21"W; Fig. 3A, locality 2), CNP-E 259, 1 left dentary; CNP-E 260, left and right dentaries; CNP-E 261, 1 palate and 1 left dentary; CNP-E 262, 3 left dentaries and 1 right dentary; CNP-E 263, left and right dentaries; CNP-E 264, 3 left dentaries; CNP-E 265, an owl pellet containing cranial and postcranial remains of 1 individual; CNP-E 266, left and right dentaries; CNP-E 293, 1

palate. Las Plumas Rockshelter (43°47'25"S, 67°18'08"W; Fig. 3A, locality 3), CNP-E 334, 3 anterior fragments of skulls, 2 left dentaries, and 2 right dentaries. De la Virgen Cave (43°42'10"S, 66°27'44"W; Fig. 3A, locality 4), CNP-E 292, 1 left dentary. Caolineria Dique Ameghino Cave (43°40'48"S, 66°25'26"W; Fig. 3A, locality 5), CNP-E 324, 1 right dentary; CNP-E 325, 1 right dentary; CNP-E 326, 1 right maxillary.

Geographical and chronological distribution.—The living population is only known from the type locality and surroundings. Fossil remains are known from the middle and lower course of the Chubut River (Fig. 3A; Udrizar Sauthier et al. 2009; Pardiñas et al. 2012).

Etymology.—In homage both to Néstor C. Kirchner (1950–2010; General Secretary of the Union of South American Nations [UNASUR] until his death in 2010) and Cristina E. Fernández de Kirchner (born in 1953), Argentinean politicians who served as the 52th (2003–2007) and 53rd–54th (2007–present) presidents of Argentina, respectively. Kirchners' presidencies were characterized by an active policy of science promotion, budget increase, and scientist repatriation that include the creation of the Ministerio de Ciencia, Tecnología e Innovación Productiva.

Diagnosis.—A species of *Tympanoctomys* slightly smaller than *T. barrerae* (head and body ~130 mm; tail ~114 mm) characterized by a unique combination of traits including less-haired and proportionally shorter bicolored tail (~43–50% of head and body length); general coloration pale brown above and whitish to white below; hind legs and forelegs whitish; more bowed dorsal profile of the skull; nasals posteriorly cuneate; supraoccipital without lateral wings; p4 with a very shallow anteroflexid and a conspicuous protoflexid; m3 8-shaped and almost similar in morphology to m2; sperm with heads of ~11.7 × 9.5 μm.

Measurements of the holotype (in mm).—Total length = 250; length of tail = 120; length of hind foot = 35; length of ear = 15; weight = 80 g; condylobasal length = 33.70; rostral width = 6.62; zygomatic breadth = 18.91; interorbital breadth = 7.39; nasal length = 13.60; nasal width = 4.59; frontal length = 10.40; width of the inferior root of the zygomatic arch = 2.37; length of upper diastema = 9.13; length of the incisive foramen = 3.56; width of the incisive foramen = 1.43; length of upper toothrow = 5.43; length of tympanic bullae = 17.65; width of tympanic bullae = 8.13; width of braincase = 21.94; foramen magnum width = 4.60; foramen magnum height = 5.89; skull case height from the tympanic bullae = 17.06; length of mandible = 20.03; length of lower toothrow = 5.43. Measurements of paratypes are given in Table 1. Measurements of fossil specimens were reported in Udrizar Sauthier et al. (2009:table 1).

Morphological description.—*Tympanoctomys kirchnerorum* is a medium-sized octodontid rodent (head and body length ~130 mm) with relatively long tail (~114 mm) in the context of the family (Fig. 1). Dorsal pelage of the head and body composed of individual hairs of gray bases and pale brown tips (~13 mm) intermixed with long (~20 mm), black guard hairs; flanks and nose paler; venter whitish to pale cream and sharply demarcated from the dorsum; individual hairs (~10 mm) pure

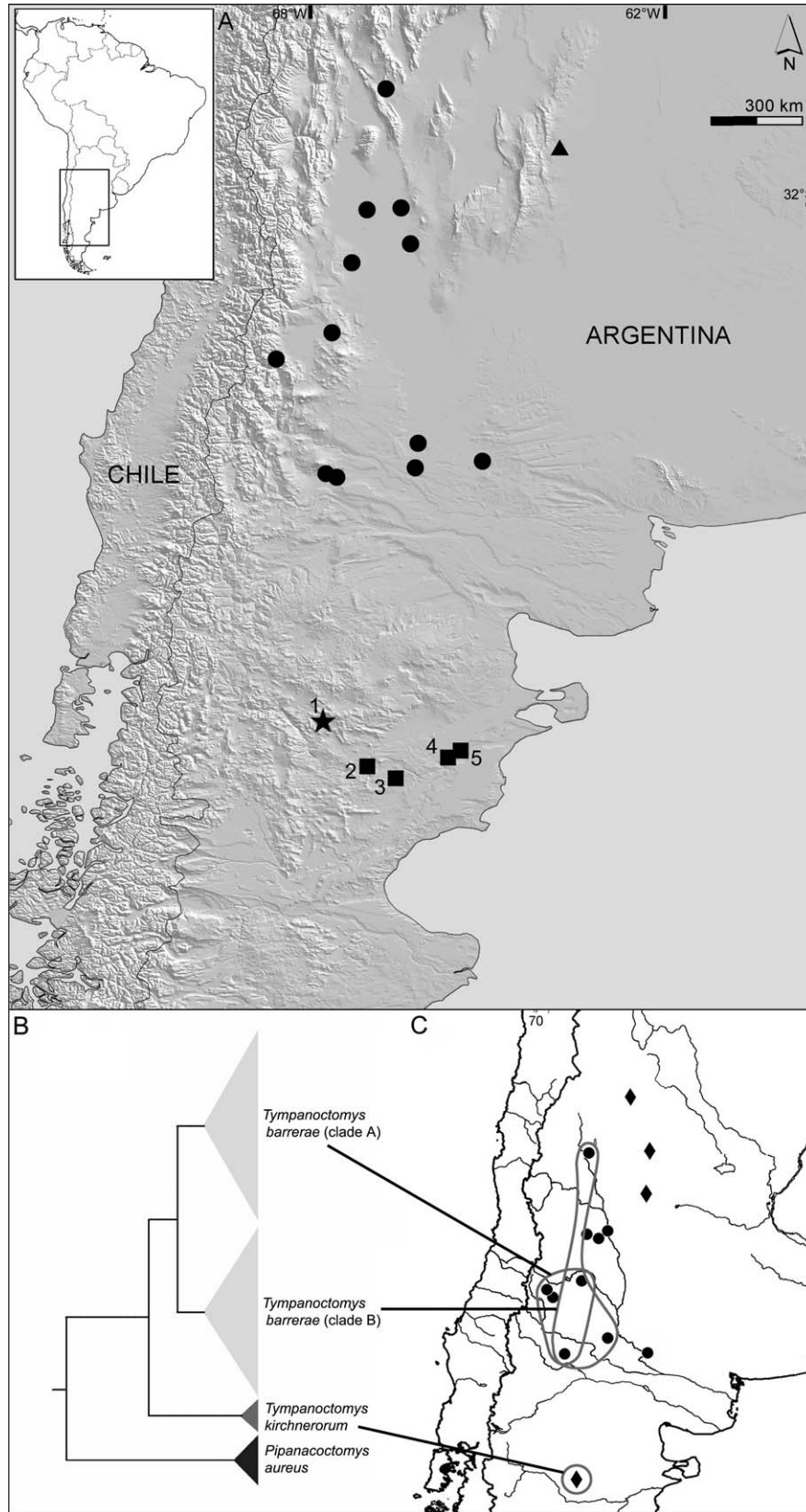


FIG. 3.—A) Geographic distribution of *Tympanoctomys* in Argentina. For the reference of the numbers see the main text. The type locality of *T. kirchnerorum*, n. sp., is indicated with a star, fossil localities for this species are marked with squares, dots depict recent occurrences for *T. barrerae* (after Ojeda et al. 2007), and the triangle plots the type locality of †*T. cordubensis*. B) Simplified mitochondrial DNA tree (after Gallardo et al. 2013). C) Geographical distribution of *T. barrerae* (dots) and the constellation of living and fossil forms (diamonds); see the “Discussion” for a full explanation.

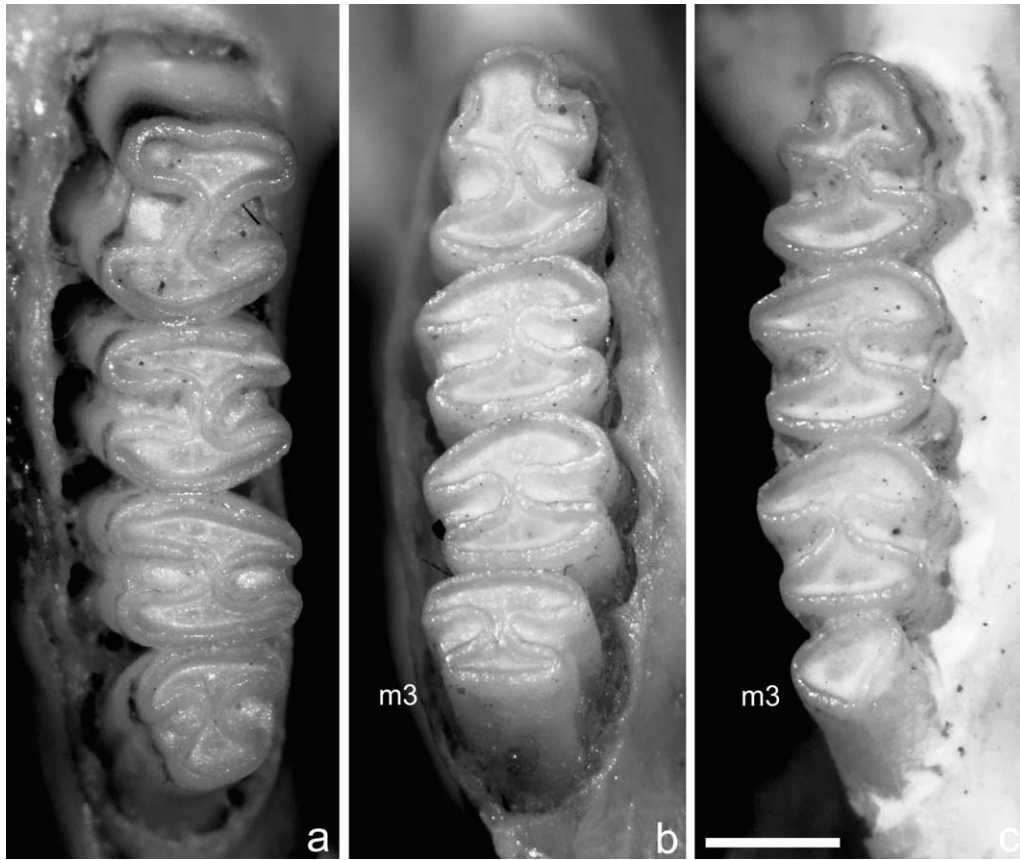


FIG. 4.—Occlusal view of upper and lower molars in *Tympanoctomys*: a) left upper and b) right lower tooththrows of *T. kirchnerorum*, n. sp., from central Chubut Province, Argentina (CNP 1862; holotype); and c) right lower tooththrow of *T. barrerae* (MACN 39–947). Note the trenchant difference between the 8-shaped 3rd lower molar (m3) in *T. kirchnerorum* and the comma-shaped m3 in *T. barrerae*. Scale = 1 mm.

white on belly and the circumgenital region and gray based with white to pale cream tips on throat, between the forelimbs, and on abdomen; mystacial vibrissae abundant (up to 30 on each side), including some short (~35 mm) and blackish and others long (~60 mm), thicker and blackish to whitish or basally blackish and distally whitish; supraorbital vibrissae in number of 2 or 3, 1 of them reaching the exterior edge of the ear; genal vibrissae up to 4 and reach the base of the ear; bristle bundles well developed and mostly composed of thick white hairs; ears small and blackish, with a tuft of whitish, hispid hairs on their base, covering the anterior half of the concha; tail densely haired, with a narrow stripe of blackish hairs above and pale cream below, with its distal ~2.5 cm blackish all around and ending in a brush of long, blackish hairs (~15–20 mm); forefeet and hind feet dorsally covered by short, thick, whitish hairs; long and whitish fringes of hairs present on both sides of hind feet; nail tufts whitish, hispid, and long, both on forefoot and hind foot, almost entirely hiding the claw on each digit; claws well developed and open from its base; soles naked and squamated.

Skull broadly built, nearly piriform in dorsal outline and bowed in lateral profile; nasals short, dorsally flat, and strongly acuminate to the posterior end; frontals divergent backward, with sharp edges, flat on the anterior portion and slightly inflated posteriorly; postorbital processes small; lacrimal bones

small and subsquared in outline, attached to the maxilla and frontal trough an almost orthogonal suture; frontoparietal suture rounded; parietals inflated; epitympanic sinuses evident in dorsal view, nearly squared in outline and with well-defined boundaries; supraoccipital with a moderate to well-marked medial crest and narrow lateral supraorbital process flanking the epitympanic sinus; contact line between the supraoccipital and the ectotympanic nearly straight; gnathic process of the premaxilla moderate in size, not exceeding the anteriormost point of nasals; diastema high and well defined; infraorbital foramen reniform in anterior view, groove and flange for infraorbital nerves moderately defined; jugal fossa short, high, well excavated, and with a conspicuous posteroventral process; maxillary arch relatively broad and vertical, giving an anterior square shape to the orbital cavity; suture between jugal and zygomatic process of maxillary markedly concave on its dorsal portion, and straight and strongly oriented backward below; suture between jugal and squamosal nearly horizontal; para-orbital apophysis small and completely formed by the squamosal; auditory bullae large and rounded, with a large and subcircular auditory meatus and contacting dorsally the hamular process of the squamosal and the supraoccipital; reduced mastoid process present behind the auditory meatus; interpremaxillar foramen conspicuous and “buttonhole”; incisive foramina elongated, with a well-developed palatine

TABLE 1.—Weights (in g) and measurements (in mm) of paratypes of *Tympanoctomys kirchnerorum*, n. sp., from central Chubut Province, Argentina.

	CNP 2386 ^a	CNP 2387 ^a	CNP 2503 ^b	CNP 2504 ^a	CNP 2505 ^a	CNP 3632 ^a
Weight (g)	56	50	—	74	69	68
Total length	250	222	—	256	237	245
Length of tail	114	111	—	112	112	113
Length of hind foot	30	29	—	33	33	30
Length of ear	15	15	—	14	14	14
Condylbasal length	30.46	30.31	27.21	34.17	32.54	—
Rostral width	5.94	5.97	5.65	5.86	6.16	—
Zygomatic breadth	17.17	17.16	16.72	18.52	17.73	—
Interorbital breadth	6.87	6.9	6.92	7.78	7.12	—
Nasal length	11.43	11.55	10.14	13.2	12.64	—
Nasal width	4.19	4.29	4.4	4.89	4.31	—
Frontal length	10.9	10.9	7.97	10.11	9.96	—
Width of the inferior root of the zygomatic arch	1.99	2.01	1.76	2.39	2.19	—
Length of upper diastema	7.66	7.7	6.96	9.29	8.18	—
Length of the incisive foramen	3.26	2.71	3.47	3.61	3.1	—
Width of the incisive foramen	1.77	1.72	1.9	1.76	1.55	—
Length of upper toothrow	5.42	5.34	5.04	5.43	5.71	—
Length of tympanic bullae	16.1	16.15	13.35	17.63	16.74	—
Width of tympanic bullae	7.54	7.64	6.42	7.54	7.55	—
Width of braincase	20.45	20.49	17.31	20.78	19.97	—
Foramen magnum width	4.22	5.37	3.8	4.47	4.77	—
Foramen magnum height	6.41	6.3	6.07	5.46	5.97	—
Skull case height from the tympanic bullae	16.1	15.98	14.16	16.38	15.88	—
Length of mandible	17.68	17.75	16.78	19.9	19.57	—
Length of lower toothrow	5.24	5.14	5.39	5.36	5.5	—

^a Adult animals.^b Young animal.

process of the premaxilla that forms a sharp ridge protruding from the premaxilla; palatine processes of the maxilla smaller and only extend one-third of the length of the incisive foramen; 2 small, symmetric or asymmetric foramina, located behind the incisive foramen; inferior root of the zygomatic with a conspicuous tubercle and a fossa for the origin of the muscle masseter superficialis; palate short, not extended beyond the posterior lobe of the M1; mesopterygoid fossa deeply excavated and V-shaped; presphenoid and basisphenoid wide; auditory bulla anteriorly expanded, which gives the appearance of an anterior convergence; internal septa numerous and evident in external view; basioccipital has an inverted Y-shape; foramen magnum elongated and somewhat inclined; paroccipital processes well developed, thin, and attached to the posterior internal portion of the auditory bulla (Fig. 2).

Mandible short and robust; diastema moderately excavated; plane defined by the occlusal surface of molar series slightly above the incisor alveolus; notch for the insertion of the anterior medial masseter muscle well expressed and lies just below the anterior half of p4; masseteric ridges sharply demarcated; capsular projection small and lies below coronoid process; coronoid short, turned backward, and slightly oriented to the labial side; condyloid process broad in lateral view, placed above the occlusal plane but slightly below the coronoid; angular process stylized, filiform, and more posteriorly projected than condyloid; semilunar notch well excavated, nearly symmetric, and C-shaped (Fig. 2).

Upper incisors opisthodont, robust and wide (~1.5 mm) and without grooves; from the outer edge, one-third of the enamel is white and the remainder is orange; P4–M3 8-shaped; main

TABLE 2.—Selected traits for a morphological comparison among *Pipanaoctomys*, *Salinoctomys*, and *Tympanoctomys*.

	<i>Pipanaoctomys aureus</i>	<i>Salinoctomys loschalcherosorum</i>	<i>Tympanoctomys barrerae</i>	<i>Tympanoctomys kirchnerorum</i> , n. sp.
Tip of tail	Pencil small	Pencil large	Pencil large	Pencil medium
Bristle bundles	Not well developed	Not well developed	Well developed	Well developed
Postorbital process	Large	Small	Small	Small
Length of palate	Extending to posterior border of M2	Extending to mid M2	Extending to posterior border of M1–mid M2	Extending to posterior border of M1–mid M2
Incisive foramina	Edges raised	Edges not raised	Edges not raised	Edges not raised
Infraorbital canal	Distinct groove and flange present	Distinct groove and flange present	No distinct groove and flange for infraorbital nerves	No distinct groove and flange for infraorbital nerves
Shape of m3	Comma-shaped	Comma-shaped	Comma-shaped	8-shaped

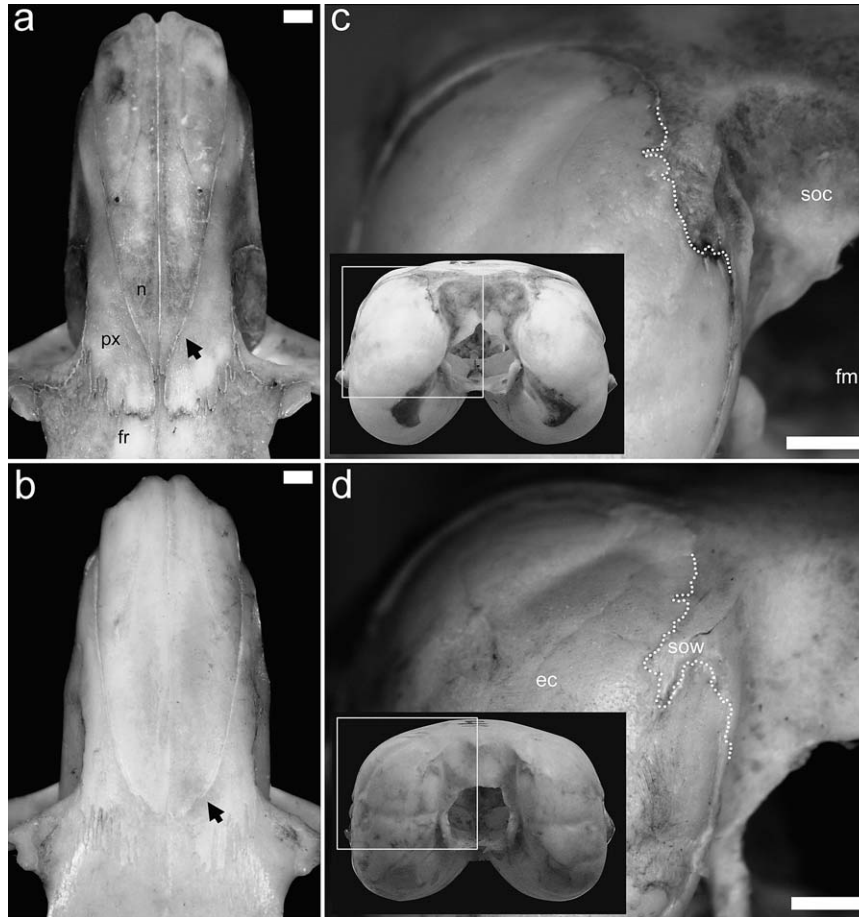


FIG. 5.—Cranial differences between *Tympanoctomys kirchnerorum*, n. sp., from central Chubut Province, Argentina (CNP 1862; holotype), and *T. barrerae* (MACN 39–947): a and b nasal and c and d supraoccipital morphologies. The arrows point to the acuminate end of the nasal (n) in a) *T. kirchnerorum* versus the barrel-shaped outline in b) *T. barrerae*. The dotted line highlights the suture between the supraoccipital (soc) and the ectotympanic (ec), uncomplicated in c) *T. kirchnerorum* versus expanded trough a lateral wing (sow) in d) *T. barrerae*. Additional acronyms: fm, foramen magnum; fr, frontal; px, premaxilla. Scale = 1 mm.

cusps opposite and nearly equal in size on each tooth; P4 slightly larger than M1–3, with the anterior face smoothly concave; mesoflexus well excavated and posteriorly oriented; hypoflexus broad and deep and almost perpendicular to the tooth axis; posterior border of the P4 more rounded than in M1–2; M1–2 similar in shape, with deeply excavated hypo- and mesoflexus; M3 shorter and narrower than M1–2, with its posterior lobe (hypocone–metacone) smaller and nearly rounded (Fig. 2).

Lower incisors wide (~1.7 mm), with orange enamel and dentine fissure Y-shaped; p4 with a rounded procingulum, very shallow anteroflexid, and a well-developed protoflexid; metaconid slightly larger than the protoconid; mesoflexid and hypoflexid deeply excavated, the former nearly perpendicular to the tooth axis and the 2nd slightly oriented forward; hypoconid and entoconid equal in size; posterior border of p4 smoothly rounded; m1–3 8-shaped; protoconid–metaconid slightly broader than hypoconid–entoconid; posterior face of hypoconid–entoconid on m1–3 relatively straight; mesoflexid and hypoflexid deeply infolded and slightly oriented forward.

Sperm morphology.—Sperm of *T. kirchnerorum* are smaller in size but similar in shape to those of *T. barrerae*. They have a paddlelike, truncated head; mean head length, mean head width, and mean tail length (\pm SD) are $11.76 \pm 1.8 \mu\text{m}$, $9.56 \pm 0.72 \mu\text{m}$, and $55.49 \pm 1.78 \mu\text{m}$, respectively. The ridge separating the nucleolus from the acrosomal tip of the head (measured from tail implantation) is at 18–22% of the head length (Gallardo et al. 2009:figure 2b).

Morphological comparisons.—*Tympanoctomys kirchnerorum* is easily distinguishable from all other members of the clade that includes *Pipanaoctomys*, *Salinoctomys*, and *Tympanoctomys* (cf. Mares et al. 2000; Gallardo et al. 2013) by its 8-shaped m3 (Fig. 4). Main differences with *Pipanaoctomys aureus*, *Salinoctomys loschalcherosorum*, and *T. barrerae* are summarized in Table 2. The extinct *A. castellanosi* has the P4–M2 with the posterior lobe not labially extended and with a deep hypoflexus (P4–M2 with transverse lobes and persistent flexi in *Tympanoctomys* spp.). As it is currently recognized, *T. kirchnerorum* is the 3rd known—and 2nd living—species in the genus *Tympanoctomys*. In

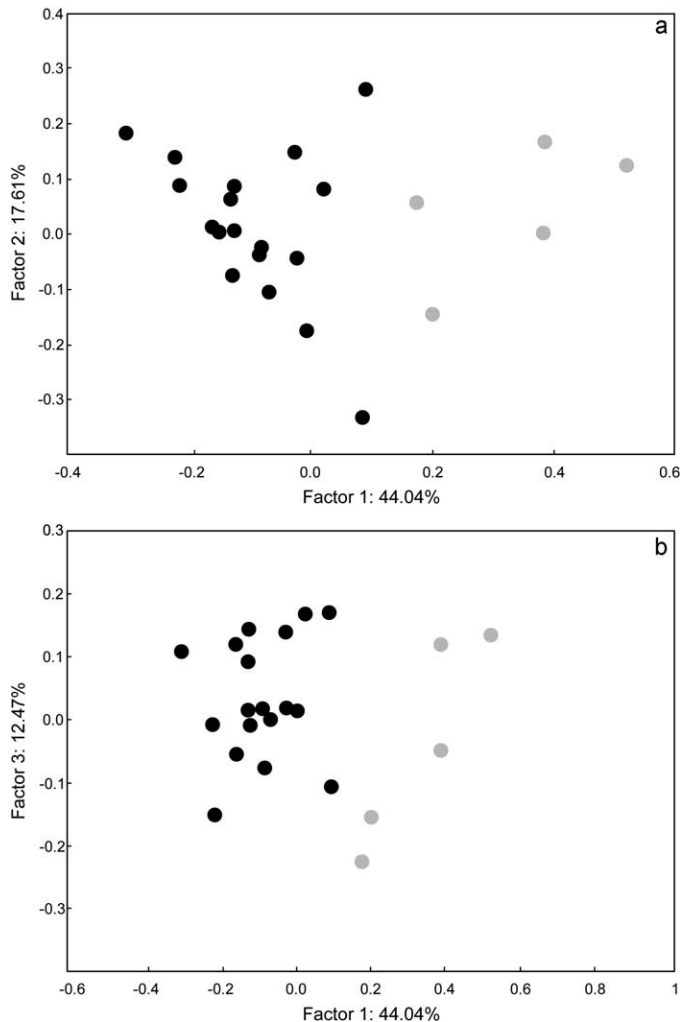


FIG. 6.—Specimen scores of adult individuals of *Tympanoctomys kirchnerorum*, n. sp., from central Chubut Province, Argentina (gray dots), and *T. barrerae* (black dots) for principal components a) 1 and 2 and b) 1 and 3 extracted from the variance–covariance matrix of 20 craniodental measurements.

comparison to *T. barrerae*, *T. kirchnerorum* is slightly smaller and has a much yellower coloration (reddish brown in *T. barrerae*) and the tail is slightly shorter (~43–50% of head and body length versus ~49–53% [cf. Diaz et al. 2000]) and less brushy. Cranially, the more conspicuous differences between both species are in nasal and supraoccipital morphology (Fig. 5). The former are narrow, strongly acuminate backward, and less curved in lateral profile in *T. kirchnerorum* (Fig. 5a), whereas *T. barrerae* has barrel-shaped nasals in outline with more-curved dorsal profile (Fig. 5b). With respect to the latter, *T. kirchnerorum* lacks lateral expansions of the supraoccipital (Fig. 5c). In turn, in *T. barrerae* this bone is laterally expanded through a wing that more extensively covers the ectotympanic (Fig. 5d). Morphometric differences are evident in principal component analysis, where the first 3 principal components summarized 74.12% of the total variation (Fig. 6). Loadings of the 20 characters analyzed along each of the first 3 components are shown in Table 3. Differences in size and morphology of

TABLE 3.—Results of principal component analysis of 20 craniodental measurements of adult specimens of *Tympanoctomys* ($n = 23$).

	PC1	PC2	PC3
Condylbasal length	-0.04	0.00	-0.01
Rostral width	-0.04	-0.01	0.00
Zygomatic breadth	-0.04	-0.01	-0.01
Interorbital breadth	-0.02	0.00	-0.01
Nasal length	-0.02	-0.01	-0.02
Nasal width	-0.03	-0.02	-0.03
Frontal length	-0.04	0.01	0.02
Width of the inferior root of the zygomatic arch	0.01	-0.01	-0.07
Length of upper diastema	-0.02	-0.01	-0.03
Length of the incisive foramen	-0.15	-0.03	0.02
Width of the incisive foramen	-0.06	0.12	0.00
Length of upper toothrow	-0.02	0.01	-0.01
Length of tympanic bullae	-0.04	0.00	-0.01
Width of tympanic bullae	-0.03	-0.01	0.01
Width of braincase	-0.02	0.00	-0.01
Foramen magnum width	-0.01	-0.03	0.03
Foramen magnum height	0.00	0.00	0.04
Skull case height from the tympanic bullae	-0.03	0.00	0.00
Length of mandible	-0.04	-0.01	-0.02
Length of lower toothrow	-0.04	0.01	-0.01
Eigenvalue	0.04	0.02	0.01
% total of variance	44.04	17.61	12.47

sperm between both living species of *Tympanoctomys* were addressed by Gallardo et al. (2009). The 3rd species in the genus, the fossil *T. cordubensis*, is only known from a few fragmentary dentaries; this form shows a comma-shaped m3 that clearly distinguishes it from *T. kirchnerorum*. In addition, †*T. cordubensis* has a larger genial process (Verzi et al. 2002). The anatomy of the postcranial skeleton of *T. kirchnerorum* and its comparison to *P. aureus*, *S. loschalchalersorum*, and *T. barrerae* was addressed by Pérez (2013); this author found several similarities between the new Patagonian species and *P. aureus*.

Karyology.—The biarmed, 102-chromosome karyotype of *T. kirchnerorum*, obtained in the field, is similar to that of *T. barrerae* in its overall appearance. It is formed by approximately 32 pairs of metacentric to submetacentric chromosomes, and 18 pairs of subtelocentric chromosomes. The sex chromosomes could not be discriminated but because of their evolutionary conservatism, probably resemble those of *T. barrerae* (Suárez-Villota et al. 2012).

Phylogeny.—The phylogenetic and phylogeographical patterns of 7 populations of *Tympanoctomys* (including those of Chubut) and its allied taxa (*P. aureus*, *Octomys mimax*, and outgroups) were studied through a 1,075–base pair fragment of cytochrome-*b* and cytochrome oxidase by Gallardo et al. (2013). The Bayesian and the maximum-likelihood analyses of these matrilineal markers recovered similar consensus topologies that clearly discriminate between diploid (*O. mimax* + outgroup) and tetraploid (*P. aureus* + *Tympanoctomys*) lineages. In addition, 3 well-supported mitochondrial lineages were recovered within *Tympanoctomys*. The 9 specimens of *T. kirchnerorum* analyzed

formed a reciprocally monophyletic, well-discriminated lineage. This group is estimated to have diverged from the other lineages at the Daniglacial of middle Pleistocene, at approximately 1.47 mya, whereas the other lineages of *T. barrerae* diverged around 1.02 mya (Gallardo et al. 2013).

Habitat and natural history.—*Tympanoctomys kirchnerorum* inhabits sandy terrains in a general landscape of badlands (Gallardo et al. 2009). The type locality of *T. kirchnerorum* is found within the *Chuquiraga avellanadae* steppe of the Central District of the Patagónica Phytogeographic Province (León et al. 1998). Plant cover near its caves is sparse, consisting mostly of low shrubs, such as *Atriplex* sp., *C. avellanadae*, *Prosopis* sp., *Prosopidastrum* sp., and *Schinus johnstonii*. Burrows of this species are easily recognizable by their fairly typical semicircular entrances of ~10 cm high, well curved dorsally and flat below, usually placed under bushes of the genus *Atriplex*. Unlike northern salt flats, where the sagebrushes *Atriplex* and *Suaeda* are the dominant species (Ojeda et al. 2007), the former is a minor component of shrubby communities in central Patagonia. However, *Atriplex* is most abundant in sandy depressions where *T. kirchnerorum* was trapped than in nearby places where this rodent is absent. Scarce signs of past burrowing activity were observed in overgrazed areas with compacted and disturbed sandy soils (Gallardo et al. 2009). Other small mammals found together with *T. kirchnerorum* in owl pellet samples collected at the type locality included the didelphid marsupial *Lestodelphys halli*; the cricetid rodents *Akodon iniscatus*, *Eligmodontia* sp., *Euneomys chinchilloides*, *Graomys griseoflavus*, and *Reithrodon auritus*; and the caviomorph rodents *Microcavia australis* and *Ctenomys* sp.

DISCUSSION

The discovery of a new species of mammal from Patagonia is not totally unexpected, taking into account that this vast territory is poorly explored from a biological point of view (Lessa et al. 2012). In fact, a moderately well-surveyed area such as the ecotone and forests of the Andean piedmont rendered several new species in the last few decades (e.g., *Aconaemys sagei* Pearson, 1984; *Ctenomys sociabilis* Pearson and Christie, 1985; and *C. coyhaiquensis* Kelt and Gallardo, 1994). *T. kirchnerorum* is, however, the 1st addition to the fauna of the extensive tablelands of extra-Andean Patagonia in the last half-century. The last biological entity to be described from the rocky hills of central Patagonia also was a caviomorph rodent, *Lagidium viscacia sumuncurensis* Crespo, 1963. A decade of extensive fieldwork in the southern portion of South America resulted in numerous new locality records that greatly expanded our knowledge about biogeography and diversity gradients (e.g., Pardiñas et al. 2003, 2008, 2011; Formoso et al. 2011; Udrizar Sauthier et al. 2011; Lessa et al. 2012).

Most of the increase in basic information came from the analysis of owl pellet deposits; in this context, it is worth summarizing how the new species reported here was discovered. In an early stage of this research, Holocene sites

with fossil remains of *Tympanoctomys* were found along the Chubut River (Udrizar Sauthier 2009; Udrizar Sauthier et al. 2009; Pardiñas et al. 2012). Later, the genus was recorded in a Recent owl pellet sample (CNP-E 333) collected near Los Adobes. Guided by this finding, subsequent trappings allowed us to collect animals formerly reported as *T. barrerae* (Gallardo et al. 2009; Ojeda 2010). More in-depth morphological comparisons indicated the distinctiveness of these specimens, living as well as fossils, a perception reinforced by molecular data (Gallardo et al. 2013).

Tympanoctomys was erected by Yepes (1942) based on the species *Octomys barrerae* Lawrence, 1941. Early in the 1980s (e.g., Woods 1982, 1984; Reig 1986), *Tympanoctomys* was considered a synonym of *Octomys*, reinserting Lawrence's original view. During subsequent decades *Tympanoctomys* remained poorly known, being restricted to few localities in Mendoza and La Pampa provinces (De Santis et al. 1991). The last 2 decades, in contrast, included numerous contributions centered on this rodent, ranging from additional recording localities (e.g., Ojeda et al. 2007) to anatomical and physiological adaptations (e.g., Diaz and Ojeda 1999; Berman 2003), and ecological works (Ojeda et al. 1996). At least in part, the renewed interest around this species' biology coincides with the discovery of its allotetraploid origin (Gallardo et al. 2006; Suárez-Villota et al. 2012). At about the same time, Mares et al. (2000) described *Pipanaoctomys* and *Salinoctomys*, 2 monotypic genera closely related to *Tympanoctomys*. Díaz and Verzi (2006) dismissed the proposed differences between these 2 genera and *Tympanoctomys*, considering them in the synonymy of the latter. Although this issue is not fully resolved it is worth discussing the evolutionary scenario depicted by *Tympanoctomys* and related taxa. With the recognition of the new Patagonian species described here, we now have a widespread species—that is, *T. barrerae*, covering about 10° of latitude—surrounded by a constellation of restricted and isolated forms, including living as well as fossil ones (Figs. 3B and 3C). Indeed, phylogeographic patterns strongly suggest a causal connection with the Quaternary cycling events that made a southward colonization or range expansion possible for *Tympanoctomys*. These events could have given rise to isolated populations, such as *T. kirchnerorum*, an ancient lineage left isolated in a later northward range shift fuelled by glaciations. In fact, phylogenetic and phylogeographic analyses depict *T. kirchnerorum* as a species whose divergence time from *T. barrerae* occurred during the Daniglacial episode, after the Great Patagonian Glaciation, approximately 1.47 mya (Gallardo et al. 2013).

Fossil remains of *T. kirchnerorum* were recovered in 4 paleontological sites of entral Chubut Province (Fig. 3A; Udrizar Sauthier et al. 2009; Pardiñas et al. 2012), indicating the occurrence of late Holocene populations of this species along the middle and lower course of the Chubut River. No living populations were found at this same general area, involving at least 200 linear kilometers along the river, despite a decade of field efforts (cf. Udrizar Sauthier 2009). The

plausible extirpation of *T. kirchnerorum* from the Chubut River valley appears to be a negative result of the ovine overgrazing, massively introduced at the beginning of the 20th century, and the subsequent packing of the soil (Pardiñas et al. 2012 and references therein).

Late Holocene octodontid extinctions in southern South America are relatively well documented, especially in Chile (Hutterer 1994; Simonetti 1994; Saavedra and Simonetti 2003). To date we prefer to consider *T. kirchnerorum* as vulnerable, because the only known population is included within an area that is being intensively prospected for large-scale uranium mining and where the exploitation of this mineral, given its strategic value as a resource, is imminent.

With the results of the present paper, at least 2 species of *Tympanoctomys* are present in Patagonia (Fig. 3A). This is a not a minor issue, because Patagonian populations of both *T. barrerae* and *T. kirchnerorum* were discovered in the last 8 years (Ojeda et al. 2007). The caviomorph radiation in southern South America was traditionally viewed as species poor, at least when contrasted with those of other groups of rodents (Mares and Ojeda 1982). Our studies and those of other researchers suggest a different scenario, one where some groups are beginning to be better understood in their specific diversity. For example new approaches to the systematics of *Aconaemys* suggest a diversity at least twice that traditionally envisioned (Guzmán Sandoval 2009). In the same way, molecular phylogenetic studies in *Ctenomys* also indicate an important theater for diversification of the genus in southern South America (Parada 2007; Parada et al. 2011). In this context, caviomorph rodents seem to be a suitable group to study the biotic evolution of Patagonia and future efforts should be made in the same direction as those recently achieved for sigmodontine rodents (e.g., Lessa et al. 2010; Pardiñas et al. 2011).

RESUMEN

Se describe una nueva especie viviente del roedor tetraploide desértico *Tympanoctomys* (Caviomorpha, Octodontidae). La nueva forma está restringida a su localidad tipo en la provincia del Chubut, Patagonia central, Argentina, si bien es conocida al menos de 4 localidades de edad Holoceno a lo largo del valle medio e inferior del río Chubut. *Tympanoctomys* sp. nov. es más pequeña que la viviente *T. barrerae*; su coloración general es amarillenta (rojiza en *T. barrerae*) y su cola es relativamente más corta (~43–50% de la longitud cabeza–cuerpo versus ~49–53% en *T. barrerae*); su cráneo y dentición están caracterizados por una combinación única de rasgos morfológicos, incluyendo nasales estrechos y posteriormente acuminados (anchos y con forma de barril en *T. barrerae*), supraoccipital no expandido lateralmente (expandido en *T. barrerae*) y tercer molar inferior en forma de 8 (en forma de coma en *T. barrerae* y †*T. cordubensis*). Diferencias morfométricas y genéticas robustecen la distinción específica de este *Tympanoctomys* patagónico endémico, también caracterizado por espermatozoides más pequeños que los de *T. barrerae*. Su reducido rango de distribución, en conjunción

con su extinción reciente en el curso medio e inferior del río Chubut y el potencial impacto de extensivos proyectos mineros en Patagonia central sugieren que esta especie enfrenta un riesgo severo de extinción en el corto plazo.

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APPENDIX I

Specimens examined of *Tympanoctomys* and *Pipanacoctomys* from the following mammal collections: MACN, Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; and UACH, Colección de Mastozoología, Universidad Austral de Chile, Valdivia, Chile.

Tympanoctomys barrerae ($n = 20$).—Argentina: Mendoza Province, El Nihuil (UACH 6957, 6958, 6959, 6960, 6962, 6964, 6965, 6966, 7093, 7094, 7097, 7098, 7099), Malargüe (MACN 39-944, 39-947, 39-948, 39-949); Neuquén Province, Salar de Añelo (UACH 7105, 7106, 7107).

Pipanacoctomys aureus ($n = 1$).—Argentina: Catamarca Province, Salar de Pipanaco (UACH 1641).