

Ctenomys mendocinus.

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***Ctenomys mendocinus* Philippi, 1869**

Mendocino Tuco-tuco

Ctenomys mendocina Philippi, 1869:38. Type locality “Mendoza” = Mendoza Province, Argentina.

Ctenomys magellanicus: Burmeister, 1879:239–240. Not *Ctenomys magellanicus* Bennett, 1836.

Ctenomys mendocinus: Philippi, 1896:17. First use of current name combination and correction of gender agreement.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricognathi, superfamily Octodontoidea, family Ctenomyidae, genus *Ctenomys* Blainville, 1826. *C. mendocinus* is monotypic (Rosi et al. 2002).

DIAGNOSIS. *Ctenomys mendocinus* (Fig. 1) can be distinguished from most medium-sized neighboring congeners by its dorsal pelage, which is light brown to reddish gray with transverse black waves along back of neck that disappear toward dirty white ventral region and by its whitish tail with dorsal median line of longer black hairs on apical half (Philippi 1869). Tail of *C. mendocinus* is shorter than tails of nearest geographical congeners *C. eremophilus* and *C. validus*. Skull of *C. mendocinus* (Fig. 2) is smaller than skull of *C. validus*, larger than that of *C. eremophilus* (Rosi et al. 1992b), and flatter and broader than those of neighboring congeners from La Pampa (*C. azarae*—Thomas 1903) and San Juan Provinces (*C. johannis*, *C. tulduco*—Thomas 1921a, 1921b). *C. mendocinus* is smaller than *C. johannis* and has larger cheekteeth (Thomas 1921b). Lateral borders of palate of *C. mendocinus* are separated more from rows of cheekteeth than those of *C. azarae* (Thomas 1903), and incisors are broader with darker fronts. Bullae of *C. mendocinus* differ markedly from long, low, and narrow bullae of *C. pontifex* (Thomas 1918) and are slightly smaller than bullae of *C. azarae*, *C. johannis*, and *C. tulduco* (Thomas 1903, 1921a, 1921b).

GENERAL CHARACTERS. *Ctenomys mendocinus* is a medium-sized tuco-tuco (Ellerman 1940; Nevo 1999; Reig et al. 1990; Stein 2000; Weir 1974). Body is robust and without a noticeable neck. Limbs are short. Fringes of stiff, coarse hairs edge the digits and broad feet and form comb-like bristles on claws of hind feet. Soles of feet are naked with large pads. Forefeet have long claws. External ears are small. Lips close behind incisors. Eyes are small to medium in size and positioned dorsally on head. Tail is sparsely covered with hair and represents ca. 46% of length of head and body (Rosi et al. 2002).

Ctenomys mendocinus shares the following characters with congeners: broad rostrum, prominently ridged parietals without sagittal crest, well-developed lambdoid crest, jugals with prominent dorsally projected processes, enlarged infraorbital foramina with no canal for nerve transmission, and large bullae with flat paraoccipital processes joined to them. Mandibles have moderately developed coronoid processes and wide angular processes that flare outwardly. Cheekteeth are kidney-shaped; 3rd molars are vestigial. Upper incisors are nearly orthodont and roots extend to start of cheekteeth (Ellerman 1940). Enamel of incisors is dark orange (Stein 2000).

Means and parenthetical ranges of selected external and cranial measurements (in mm) for 18 adult females and 18 adult males, respectively, from near type locality (Rosi et al. 2002) are: total length, 247.3 (230–262), 262.2 (237–280); length of tail, 77.4 (70–84), 82.2 (72–91); length of hind foot, 34.1 (32–36), 36.4 (34–38); length of ear, 7.5 (6–9), 8.4 (7–10); greatest length of cranium, 41.0 (39–43), 44.8 (41–47); basal length of cranium, 39.7 (37–41), 43.5 (40–45); length of frontal, 12.7 (11–14), 13.1 (11–15); length of nasals, 13.6 (13–15), 14.9 (12–16); length of incisive foramen,

6.1 (5–7), 6.5 (6–7); length of maxillary diastema, 10.4 (9–12), 11.7 (10–14); greatest breadth of braincase, 16.8 (16–18), 17.5 (17–19); zygomatic breadth, 24.0 (23–26), 26.1 (24–28); breadth of auditory bullae, 7.8 (7–8), 8.3 (8–9); breadth of nasals, 5.5 (5–6), 6.1 (5–7); height of cranium, 13.5 (12–14), 14.5 (13–16); total length of mandible, 28.9 (28–31), 32.3 (30–34); breadth of mandible, 30.3 (28.8–32.5), 33.3 (30.0–35.8); and length of mandibular toothrow, 19.4 (18–21), 21.7 (20–24). Means and parenthetical ranges of body mass (in g) for the same 18 females and 18 males are 145.3 (108–200) and 180.8 (124–253), respectively. Males are larger than females in all previously mentioned external and cranial measurements except length of frontal (Rosi et al. 2002).

DISTRIBUTION. *C. mendocinus* occurs in northern and central Mendoza Province of Argentina (Fig. 3) from ca. 31°S to 34°S and from Andean Precordillera eastward across arid sub-Andean regions (Rosi et al. 2002). Records in adjoining provinces of San Luis and San Juan are scarce, and thus northern and eastern limits of distribution are not well delineated. Elevation at locations of known occurrence ranges from 460 to 3,400 m (Rosi et al. 2002). A wider geographic range (Cabrera 1961; Honacki et al. 1982; Redford and Eisenberg 1992; Woods 1993) included taxa that now are recognized as distinct species.

FOSSIL RECORD. No fossils of *C. mendocinus* are known. Subfossil remains occur in the archaeological pre-Hispanic site Agua de la Tinaja I (ca. 4,500 to 1,400 years ago—Bárcena et al. 1985). This site is located in northwestern Mendoza Province (32°28'S, 69°18'W), in the geographic distribution of living populations of *C. mendocinus*.

FORM AND FUNCTION. Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20 (Redford and Eisenberg 1992). Thickness of inner and outer layers of incisor enamel is 58.93 μ and 249.33 μ , respectively (Justo et al. 1995).

Spermatozoa of *C. mendocinus* have paddle-like asymmetrical heads with tails inserted at 1 side of the central axis. A postacrosomic process (nuclear caudal extension) originates at base of head opposite to insertion of flagellum (Vitullo et al. 1988).

Relative size of encephalic components (estimated by progression indices) and parenthetical percent volumes of brain components (Bee de Speroni 1995) are: total brain index, 199 (100%); neocortex, 552 (35.7%); cerebellum, 253 (15.9%); diencephalon, 232 (11.4%); striatum, 480 (8.7%); medulla oblongata, 126 (8.1%); hippocampus, 201 (7.9%); mesencephalon, 204 (5.7%); rhinencephalon, 63 (5.5%); olfactory bulbs, 30 (1.5%); and septum, 113 (0.9%). Relative size of neocortex indicates *C. mendocinus* is well

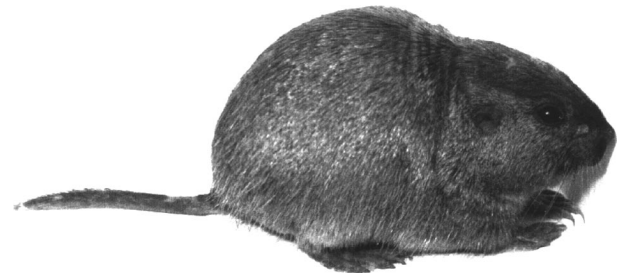


FIG. 1. Photograph of an adult female *Ctenomys mendocinus* from 20 km SW of Mendoza city, Mendoza Province, Argentina. Used with permission of the photographer D. Rosales.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Ctenomys mendocinus* (IADIZA [Argentinean Institute for Research on Arid Lands] mammal collection, CM 02503) from Mendoza Province. Greatest length of cranium is 47.0 mm.

suiting for underground life; relative sizes of cerebellum and striatum are consistent with motor abilities associated with building burrows and handling food. Olfactory bulbs and rhinencephalon are regressive in concordance with herbivorous diet. Well-developed tactile sensitivities are inferred from relative size of medulla oblongata; values for mesencephalon are indicative of visual and auditory acuity (Bee de Speroni 1995).

ONTOGENY AND REPRODUCTION. In Paramillos of Uspallata (3,000 m elevation), Mendoza Province, reproduction extends from August to February, with births occurring from December to February (Rosi et al. 1992a). Monthly percentages of preg-

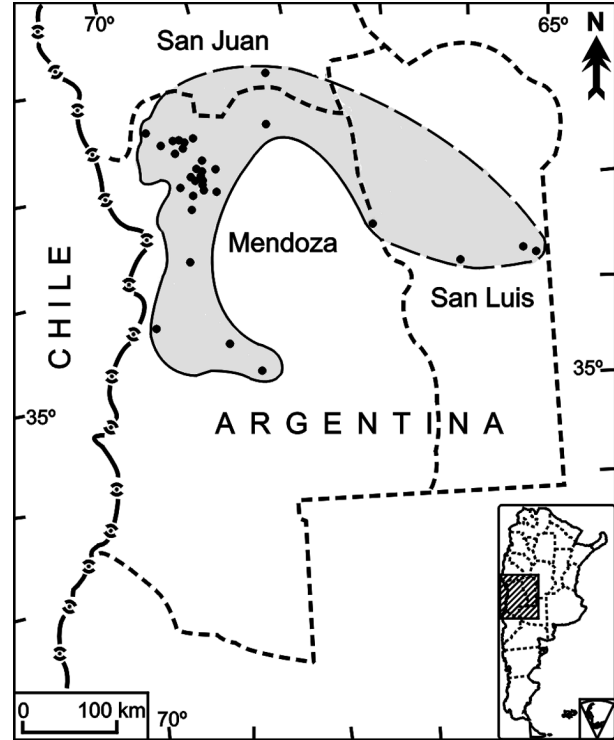


FIG. 3. Geographic distribution of *Ctenomys mendocinus*, including all published records of occurrence. Boundary line is discontinuous in San Juan and San Luis Provinces because of paucity of records. Modified from Rosi et al. (2002).

nant females during the reproductive period are highest in October (67%) and lowest in January (18%). In October and November, percent of pregnant females that gave birth in previous reproductive seasons (56% and 33%, respectively) is higher than that of females pregnant for the 1st time (11% and 17%). Most females produce 1 litter during the breeding season; ca. 10% of pregnant females captured in January show signals of lactation, indicating a 2nd pregnancy resulting from mating during postpartum or midlactation estrus. Males and females reach sexual maturity in the 1st reproductive season after their birth when they are 6–8 months old (Rosi et al. 1992a).

At a lower elevation in Cacheuta, Mendoza Province (1,330 m elevation), *C. mendocinus* has a longer reproductive period (from mid-July to March) and a larger percent of females that were pregnant from postpartum or midlactation estrus (50%—Rosi et al. 1996b). During the reproductive period, prevalence of pregnancy is highest in July (89%) and October (88%) and low (8%) in February. No pregnant females were collected in April and May. Estimated length of gestation is 3 months. Litter size, based on mean counts of embryos ($\pm SD$), is 2.9 ± 0.94 ($n = 11$) in Paramillos of Uspallata (Rosi et al. 1992a) and 2.8 ± 0.94 ($n = 27$) in Cacheuta (Rosi et al. 1996b). During the reproductive period at Cacheuta, mean length ($\pm SD$, in mm) of testes of mature males is greatest in July (14.9 ± 3.0 ; $n = 13$) and smallest in February (11.1 ± 1.39 ; $n = 13$ —Rosi et al. 1996b).

Histological sections of testes of specimens from Cacheuta (Mendoza) show increased gonadal activity in spring as evidenced by development of spermatocytes and spermatids and abundant spermatozoa in seminiferous tubules (Dacar et al. 1998). Spermatid and spermatozoid production decrease toward late summer and during fall. Some females initiate follicular development in winter; others have vascularized corpora lutea indicating pregnancy. Gonadal activity in females continues during spring and summer. Gonadal regression is apparent in the fall as evidenced by absence of follicular development beyond primary follicle stage and presence of nonvascularized corpora lutea and corpora albicans (Dacar et al. 1998).

ECOLOGY. *Ctenomys mendocinus* inhabits arid and semi-arid environments in lowlands and mountainous regions (Rosi et al.

2002). In Mendoza Province, populations occur in open scrublands in the Andean Piedmont, where *Atriplex lampa*, *Larrea cuneifolia*, and *L. divaricata* are dominant (Pearson and Lagiglia 1992; Puig et al. 1999; Rosi et al. 1992b). Populations in the Andean Precordillera of Mendoza occur in grass communities of *Stipa* associated with low shrubs such as *Adesmia horrida*, *Artemisia mendociana*, and *Senecio flaginoides* (Rosi et al. 2000). These habitats differ in percentage plant cover (80% and 25% in the Andean Piedmont and Precordillera, respectively). Mean annual precipitation in areas inhabited by *C. mendocinus* ranges from 100 to 300 mm (Puig et al. 1999; Rosi et al. 2000). In San Luis Province, *C. mendocinus* occurs in natural grasslands of *Bromus*, *Poa*, *Sorghastrum*, and *Stipa* that are degraded by cattle grazing (Rosi et al. 1992b) and on the periphery of salt flats (Braun and Mares 1995b). In San Juan Province, *C. mendocinus* occurs near sand dunes and salt flats (Braun and Mares 1995b). *C. mendocinus* occurs in soils ranging from sandy to relatively compact and composed of lithosols within a matrix of clay and silt (Rosi et al. 1992b).

Burrow systems of *C. mendocinus* from 2 habitats of Mendoza Province have a linear configuration, with a main axis from which lateral tunnels and branches fork off. The main tunnel has straight short segments; mean directional angles of consecutive segments are close to 0°. Lateral tunnels are straight tunnels that never branch off. Ca. 60% of lateral tunnels reach the surface and end in either a soil mound or a plugged hole; the remainder end in a “cul-de-sac.” Branches are tunnels with at least 1 segment and 1 lateral tunnel. Number of branches ranges from 1 to 13 per system, and number of lateral tunnels ranges from 8 to 47 per system. Whereas branches originate perpendicular to main tunnel, lateral tunnels have an ascent angle close to 40°. Mean depth of main tunnel was 0.30 m in both habitats, and total length of burrow (mean \pm SD, in m) for males and females, respectively, was 50.5 \pm 21.0 and 22.4 \pm 6.8 in the Andean Piedmont (1,125 m—Rosi et al. 1996a) and 48.3 \pm 18.2 and 41.5 \pm 9.4 in the Andean Precordillera (3,000 m—Rosi et al. 2000). Most burrows in the Precordillera have storage chambers filled with grasses. Partially collapsed tunnel sections and severe decline in plant cover in areas surrounding active burrows suggest a progressive expansion of feeding tunnels toward places with higher food availability (Puig et al. 1992; Rosi et al. 2000). Home range size (mean \pm SD, in m²) is 43.1 \pm 31.1 for males and 11.9 \pm 6.08 for females in the Piedmont habitat (Rosi et al. 1996a) and 23.7 \pm 7.4 and 21.7 \pm 6.1 in the Precordillera (Rosi et al. 2000). Average number of mounds per system (\pm SD) is 6.2 (\pm 3.08, $n = 10$) for both sexes in the Piedmont habitat (Rosi et al. 1996a) and 5.0 (\pm 1.3, $n = 6$) for females and 8.0 (\pm 5.6, $n = 6$) for males in the Precordillera (Rosi et al. 2000). Distribution of active burrow holes in the Precordillera is clumped, with a density of 221 holes/ha in fall and 52 holes/ha in spring (Puig et al. 1992). Average amount of soil removed in captivity by adults of *C. mendocinus* during digging is 215 g/min, with a ratio of removed soil to body mass of 23.39 and a mean digging speed of 0.062 cm/s (Camín et al. 1995).

Ctenomys mendocinus is herbivorous and feeds mainly on grasses (Madoery 1993; Puig et al. 1999; Rosi et al. 2003; Torres-Mura et al. 1989). In the Andean Piedmont of Mendoza, grasses dominate the diet of *C. mendocinus* throughout the year and reach highest proportions in summer (94.5%); species most consumed are *Aristida*, *Panicum*, *Poa*, *Setaria*, and *Stipa*. Shrubs, represented by *Atriplex lampa*, *Acantholippia seriphioides*, *Cassia aphylla*, *Cercidium*, and *Larrea divaricata*, are eaten mainly in winter (29.5%). Forbs and succulents are consumed in small proportions (1%—Madoery 1993). In the same environment, *C. mendocinus* consumed 33 genera of plants (65% of those present in the field—Puig et al. 1999). Only 13 genera (8 of them grasses) were eaten with a frequency $>3\%$. The large proportion of grasses in the diet (60% in winter and 98% in summer) and their use throughout the year indicates specialization on grasses. Greatest food-niche breadth (estimated by the Shannon-Wiener index, H') is obtained in winter (0.76), coincident with the highest dietary variation among individuals (49%), whereas the lowest food-niche breadth occurs in summer (0.52—Puig et al. 1999).

In a habitat of the Andean Precordillera (Mendoza Province) with 36% plant cover, *C. mendocinus* consumed 23 of 32 available plant genera, but only 6 reached frequencies $>4\%$ throughout the year (Rosi et al. 2003). Grasses are available throughout the year, with a relative cover of ca. 73%, followed by shrubs with ca. 24%. The grasses *Elymus erianthus* and *Stipa* make up ca. 80% of the

annual diet. Shrubs follow grasses in dietary importance, but most are eaten with frequencies $<4\%$. A large proportion of aerial plant material (ca. 90%) is found in stomach contents. In the Andean Precordillera, *C. mendocinus* preferentially consumes grasses, avoids shrubs, and specializes on a few food items (Rosi et al. 2003).

Herbivory by *C. mendocinus* on shrubs, estimated by percentages of cut-off stems, affects 39% of total plants in Villavicencio and 9% in Divisadero Largo Reserve (Mendoza Province). The most highly damaged species are *Larrea divaricata* (65%), *Lycium chilensis* (41%), *Junellia seriphioides* (38%), and *Menodora decemfida* (33%) in Villavicencio. The latter 3 species are most damaged in Divisadero Largo, but in lower percentages (9%, 14%, and 6%, respectively—Tort et al. 2004).

Density of *C. mendocinus* from the Andean Precordillera of Mendoza was 10 animals/ha in fall and 3.3 animals/ha in spring, with a uniform spatial distribution during both seasons (Puig et al. 1992). In fall, mean distance between capture locations (\pm SD, in m) of different individuals was 21.6 \pm 6.7 for 2 adult females, 18.1 \pm 6.7 for an adult male and an adult female, and 6.5 \pm 3.5 for an adult female and an immature female; maximum distance occurred between 2 adult males (36.8 m—Puig et al. 1992).

An equal sex ratio was found for total animals captured in 2 study populations from Mendoza Province: males represented 47.5% of total individuals ($n = 141$) in Cacheuta (Rosi et al. 1996b) and 47.2% of total individuals ($n = 89$) in Paramillos of Uspallata (Rosi et al. 1992a). In the Paramillos of Uspallata population, significant deviations from 1:1 sex ratio were detected in spring and summer (41% and 61% males, respectively). A large proportion of mature animals (ca. 72%) was recorded throughout the year for both populations. At the end of summer and early fall, 2 age groups occur: immature animals (<4 months old) born during the most recent reproductive season and mature individuals (≥ 1 year old) born in previous breeding seasons. Animals of intermediate ages (>4 months old and <1 year old) are absent because births occur only during 4 months from mid-spring to late summer (Rosi et al. 1996b).

In the arid habitats of central-western Argentina, *C. mendocinus* coexists with small and medium-sized mammals such as *Akodon molinae*, *Calomys musculus*, *Dolichotis patagonum*, *Eligmodontia typus*, *Galea musteloides*, *Graomys griseoflavus*, *Lagidium viscacia*, *Lagostomus maximus*, *Microcavia australis*, *Phyllotis xanthopygus*, *Salinomys delicatus*, *Thylamys pallidior*, and *Tympanoctomys barrerae* (Braun and Mares 1995b; Pearson and Lagiglia 1992; Rosi 1983; Torres-Mura et al. 1989).

Ctenomys mendocinus from Mendoza and San Luis Provinces harbor 5 species of lice, including 4 from the family Gyrodidae (*Gyropus parvus parvus*, *Phtheiropoios mendocinus*, *P. gracilipes*, *P. rionegrensis*) and 1 from Polyplacidae (*Eulinognathus wernicki*—Cicchino and Castro 1996; Cicchino et al. 2000; Contreras et al. 1999). *P. mendocinus* has been reported only for *C. eremophilus* and *C. mendocinus* from Mendoza (Cicchino and Castro 1998). Other ectoparasites of *C. mendocinus* include the fleas *Polygenis platensis cisandinus*, *Tiamastus longinasus*, and *Tiarapsylla argentina*; the latter is from San Rafael, Mendoza (Giménez et al. 1964; Jordan 1942).

BEHAVIOR. *Ctenomys mendocinus* is a solitary fossorial rodent with strongly territorial behavior as evidenced by capture of only 1 specimen per burrow system, even during the reproductive season (Puig et al. 1992), and absence of linking tunnels between neighboring systems (Rosi et al. 1996a, 2000). Individuals are active throughout the year, but winter snowfall and ground freezing in high mountain habitats reduce burrowing activities. At the beginning of spring when snow has melted, number of active burrow holes is 4.25 times lower than in the fall (Puig et al. 1992).

Burrowing behavior of captive *C. mendocinus* is characterized by successive repetitive series of scratching-kicking-scratching, followed by transport of removed soil through the tunnel (Camín et al. 1995). Scratching consists of rapid alternate strokes of foreclaws (5–6 strokes s⁻¹ leg⁻¹); eyes are closed. Loosened soil that accumulates below abdomen is thrown backward by strokes of hind legs (kicking). *C. mendocinus* pushes soil along tunnel with hind legs (transport). Scratching, kicking, and transport are always followed by exit from burrow. Mean duration (in s) of each behavioral pattern was scratching, 2.76; kicking, 0.77; transport, 5.68; and exit, 14.93. Transport and scratching comprised 61% of the observation period.

C. mendocinus is classified as a claw-digger because its incisors were only occasionally used while digging (Camín et al. 1995). Captive *C. mendocinus* use their tail as a prop while scratching to loosen earth (Camín et al. 1995).

Both sexes vocalize with growls and whines. Vocal, tactile, and chemical signals occur during courtship and mating (Camín 1999). Males mark the floor and lateral walls of their burrows with urine and rub their anogenital region against these surfaces. Males use female urine to assess reproductive condition.

Reproductive behavior of *C. mendocinus* involves vocalizations, a discontinuous and long courtship, long bouts of precopulatory interactions, a brief copulatory stage with lengthy intromissions, aggressive copulatory postures, and a single ejaculation (Camín 1999). Mean durations ($\pm SD$, in s) of reproductive behaviors were courtship, $847 \pm 1,056$; precopulatory interactions, 44 ± 74 ; and copulatory stage, 256 ± 200 . Precopulatory interactions included partners swaying from side to side with incisors locked together. Animals also stood on their hind feet and grasped each other's cheek with forefeet and teeth. Mutual indifference characterized postmating behavior of partners (Camín 1999).

Feeding behavior of captive *C. mendocinus* is characterized by an opportunistic harvest pattern and selective consumption pattern. Animals harvest a wide variety of plants but prefer to eat aboveground parts of grasses and generally avoid shrubs and roots (Camín and Madoery 1994). Signs of aboveground foraging, such as cut-off stems of shrubs, grasses, and cacti, occur near or around burrow openings (Camín et al. 1995; Puig et al. 1992). These signs and the large proportion of aerial plant material in the diet of *C. mendocinus* indicate that foraging on the surface is common (Rosi et al. 2003).

GENETICS. *C. mendocinus* from 3 localities of Mendoza Province (Paramillos of Uspallata, San Isidro, and Tupungato) exhibits 2 karyotypes, KMI and KMII (Massarini et al. 1991a, 1991b). Two groups of autosomes were distinguished for karyotype descriptions: "A" biarmed and "B" telocentric chromosomes. The KMI karyotype ($2n = 48$, FN = 76) was found in 1 male and 3 females from San Isidro and in 2 females from Paramillos of Uspallata. Group A contains 15 pairs of medium-sized to small chromosomes (5 pairs of subtelocentrics, 8 pairs of submetacentrics, and 2 pairs of metacentrics), and Group B contains 8 pairs of telocentric small chromosomes. Pair B4 shows a secondary constriction shared with nucleolus organizer regions. X chromosome is a small metacentric, and Y chromosome is a small subtelocentric. C-bands reveal that constitutive heterochromatin is located in short arms of all biarmed chromosomes, except pairs A5, A13, A14, and A15, in which heterochromatin is in the centromeric region. Pair A12 has heterochromatic short arms; sex chromosomes show heterochromatin in the centric region.

The KMII karyotype ($2n = 47$) found in 1 female from San Isidro (FN = 75) and 1 female from Tupungato (FN = 68) differs from KMI in pairs A1 and B2. In KMII, both homologues of pair A1 (A1a and A1b) differ in morphology and in C- and G-bands. Chromosome A1b of KMII is identical to chromosome A1b of KMI, but A1a is a large metacentric chromosome whose heterochromatin is limited to a centromeric region. One homologue of pair B2 is absent in KMII. Banding pattern of heteromorphic pair A1 reveals that this polymorphism involved at least 3 rearrangements: deletion of the heterochromatic short arm, pericentric inversion, and fusion with distal portion of B2. Differences in FN between the 2 individuals are due to deletion/amplification of heterochromatic short arms of different pairs of biarmed chromosomes.

Karyotype KMI of *C. mendocinus* exhibits high homogeneity in diploid number and C- and G-band patterns with *C. australis*, *C. azarae*, *C. porteوسي*, and *Ctenomys* from Chasicó (Province of Buenos Aires). *C. azarae*, *C. porteوسي*, and *Ctenomys* from Chasicó also share with *C. mendocinus* the pair A1 complex polymorphism and have similar variations in whole-arm heterochromatin (Massarini 1992).

REMARKS. *C. haigi*, *C. maulinus*, and *C. talarum recessus* were included as subspecies of *C. mendocinus* by Thomas (1927a, 1927b, 1929). Cabrera (1961) included 8 taxa as subspecies of *C. mendocinus* (*C. bergi*, *C. fochi*, *C. haigi*, *C. juris*, *C. occultus*, *C. pundi*, *C. talarum recessus*, and *C. tucumanus*) and considered *C. azarae* and *C. latro* synonyms of *C. mendocinus* and *C. tucumanus*, respectively. Morphological, genetic, and molecular data

show these taxa are distinct species (Contreras and Reig 1965; Gallardo 1991; Giménez et al. 1999; Massarini et al. 1991a, 1991b; Pearson 1984; Reig and Kiblicky 1969; Reig et al. 1992; Roig and Reig 1969; Slamovits et al. 2001).

The generic name *Ctenomys* is derived from the Greek *kteis* (genitive *ktenos*) meaning "raker" or "comb" (in reference to stiff hair fringes on claws of hind feet) and *mys* from the Greek meaning "mouse." The species name *mendocinus* refers to the type locality, Mendoza, Mendoza Province, Argentina (Braun and Mares 1995a). Additional vernacular epithets include Mendoza tucu-tuco, tulduque, and tunduque (Roig 1965; Woods 1993). These names make reference to the guttural "tuc-tuc" sound emitted by many *Ctenomys* species (Pearson et al. 1968).

Prior to Tate (1935), *Ctenomys* and extinct allied genera were usually included among octodontids without taxonomic hierarchy of their own (Ameghino 1889; Miller and Gidley 1918; Rovereto 1914; Rusconi 1931). Tate (1935) and then Reig (1958; Pascual et al. 1965) separated *Ctenomys* and related fossils from the remaining octodontids. This proposal persists, but with disagreement as to taxonomic rank, that is, as families Ctenomyidae and Octodontidae (Cabrera 1961; Honeycutt et al. 2003; Simpson 1945; Wood 1955; Woods 1993), subfamilies of Octodontidae (Gallardo 1997; Pascual et al. 1965; Reig 1989), or tribes of Octodontinae (McKenna and Bell 1997). Monophyly of the clade Octodontidae-Ctenomyidae is strongly supported (Gallardo and Kirsch 2001; Honeycutt et al. 2003). We consider Ctenomyidae and Octodontidae independent families.

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LITERATURE CITED

- AMEGHINO, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba* 6:1–1027.
- BÁRCENA, J. R., F. A. ROIG, AND V. G. ROIG. 1985. Aportes arqueofito-zoológicos para la Prehistoria del N.O. de la provincia de Mendoza: la excavación de Agua de la Tinaja I. *Trabajos de Prehistoria* 42:311–363.
- BEE DE SPERONI, N. 1995. Encefalización y tamaño relativo de los componentes encefálicos en *Ctenomys mendocinus* Philippi 1869 (Rodentia: Ctenomyidae). *Mastozoología Neotropical* 2:31–38.
- BENNETT, E. T. 1835 [1836]. On a new species of *Ctenomys* and other rodents collected near the Straits of Magellan by Capt. P. P. King, R. N. *Proceedings of the Zoological Society of London* 1835:189–191.
- BLAINVILLE, H. M. D. 1826. Sur une nouvelle espèce de rongeur fouisseur du Brésil. *Nouveau Bulletin des Sciences, Société Philomathique de Paris* 3:62–64.
- BRAUN, J. K., AND M. A. MARES. 1995a. The mammals of Argentina: an etymology. *Mastozoología Neotropical* 2:173–206.
- BRAUN, J. K., AND M. A. MARES. 1995b. A new genus and species of phyllotine rodent (Rodentia: Muridae: Sigmodontinae: Phyllotini) from South America. *Journal of Mammalogy* 76:504–521.
- BURMEISTER, H. 1879. Description physique de la République Argentine d'après des observations personnelles et étrangères. Paul-Emile Coni, Buenos Aires, Argentina 3(1):vi + 1–555.
- CABRERA, A. 1961. Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, *Ciencias Zoológicas* 4:309–732.
- CAMÍN, S. 1999. Mating behaviour of *Ctenomys mendocinus* (Rodentia, Ctenomyidae). *Zeitschrift für Säugetierkunde* 64:230–238.
- CAMÍN, S. R., AND L. A. MADOERY. 1994. Feeding behavior of the tucu-tuco (*Ctenomys mendocinus*): its modifications according to food availability and the changes in the harvest pattern and consumption. *Revista Chilena de Historia Natural* 67:257–263.
- CAMÍN, S., L. MADOERY, AND V. ROIG. 1995. The burrowing behavior of *Ctenomys mendocinus* (Rodentia). *Mammalia* 59:9–17.
- CICCHINO, A. C., AND D. DEL C. CASTRO. 1996. Revalidation of *Phthiropoios gracilipes* (Amblycera, Gyropidae), with re-

- marks on its synoxenism and distribution in *Ctenomys* species from Argentina (Rodentia, Ctenomyidae). *Iheringia, Série Zoológica* 81:81–86.
- CICCHINO, A. C., AND D. DEL C. CASTRO. 1998. *Phthiropoios mendocinus* sp. nov. y estado del conocimiento de las demás especies del género *Phthiropoios* Eichler, 1940 (Phthiraptera: Gyropidae) en la provincia de Mendoza, Argentina. *Gayana Zoológica* 62:183–190.
- CICCHINO, A. C., D. DEL C. CASTRO, AND J. C. BALDO. 2000. Elenco de los *Phthiraptera* (Insecta) hallados en distintas poblaciones locales de *Ctenomys* (Rodentia: Octodontidae) de Argentina, Uruguay, Paraguay, Bolivia, y Brasil. *Papéis Avulsos de Zoologia* 41:197–211.
- CONTRERAS, J. R., D. DEL C. CASTRO, AND A. A. CICCHINO. 1999. Relaciones de los Phthiraptera (Insecta, Amblycera, Gyropidae) con la evolución taxonómica de los roedores del género *Ctenomys* (Mammalia: Rodentia, Caviomorpha: Ctenomyidae). *Ciencia Siglo XXI* 2:1–32.
- CONTRERAS, J. R., AND O. A. REIG. 1965. Datos sobre la distribución del género *Ctenomys* (Rodentia, Octodontidae) en la zona costera de la provincia de Buenos Aires comprendida entre Necochea y Bahía Blanca. *Physis* 25:169–186.
- DACAR, M., S. MONGE, S. BRENGIO, AND V. ROIG. 1998. Estudio histológico en gónadas de *Ctenomys mendocinus* en la localidad de Cacheuta (Mendoza, Argentina). *Mastozoología Neotropical* 5:13–19.
- ELLERMAN, J. R. 1940. The families and genera of living rodents. Rodents other than Muridae. *British Museum (Natural History) London* 1:181–698.
- GALLARDO, M. H. 1991. Karyotypic evolution in *Ctenomys* (Rodentia, Ctenomyidae). *Journal of Mammalogy* 72:11–21.
- GALLARDO, M. H. 1997. A saltational model of karyotypic evolution in the Octodontoidea (Mammalia, Rodentia). Pp. 347–365 in *Chromosomes today* (N. Henríquez-Gil, J. S. Parker, and M. J. Puertas, eds.). Chapman & Hall, London, United Kingdom.
- GALLARDO, M. H., AND J. A. W. KIRSCH. 2001. Molecular relationships among Octodontidae (Mammalia: Rodentia: Caviomorpha). *Journal of Mammalian Evolution* 8:73–89.
- GIMÉNEZ, M. D., C. J. BIDAÚ, C. F. ARGÜELLES, AND J. R. CONTRERAS. 1999. Chromosomal characterization and relationship between two new species of *Ctenomys* (Rodentia, Ctenomyidae) from northern Córdoba province, Argentina. *Zeitschrift für Säugetierkunde* 64:91–106.
- GIMÉNEZ, D. F., C. A. CICCARELLI, AND J. M. DE LA BARRERA. 1964. Siphonaptera de Mendoza. *Anales de la Sociedad Científica Argentina* 178:125–139.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press and the Association of Systematics Collections, Lawrence, Kansas.
- HONEYCUTT, R. L., D. L. ROWE, AND M. H. GALLARDO. 2003. Molecular systematics of the South American caviomorph rodents: relationships among species and genera in the family Octodontidae. *Molecular Phylogenetics and Evolution* 26:476–489.
- JORDAN, K. 1942. On the Siphonaptera collected by Dr. J. M. de la Barrera in the province of Mendoza during 1939. *Revista del Instituto Bacteriológico "Dr. Carlos G. Malbrán"* 10:401–460.
- JUSTO, E. R., L. E. BOZZOLO, AND L. J. M. DE SANTIS. 1995. Microstructure of the enamel of the incisors of some ctenomyid and octodontid rodents (Rodentia, Caviomorpha). *Mastozoología Neotropical* 2:43–51.
- MADOERY, L. 1993. Composición botánica de la dieta del tuco-tuco (*Ctenomys mendocinus*) en el piedemonte precordillerano. *Ecología Austral* 3:49–55.
- MASSARINI, A. I. 1992. Evolución cromosómica de las especies de *Ctenomys* de la Región Pampeana y de Cuyo. Ph.D. dissertation, University of Buenos Aires, Argentina, 147 pp.
- MASSARINI, A. I., M. A. BARROS, M. O. ORTELLS, AND O. A. REIG. 1991a. Chromosomal polymorphism and small karyotypic differentiation in a group of *Ctenomys* species from central Argentina (Rodentia, Octodontidae). *Genética* 83:131–144.
- MASSARINI, A. I., M. A. BARROS, V. G. ROIG, AND O. A. REIG. 1991b. Banded karyotypes of *Ctenomys mendocinus* (Rodentia: Octodontidae) from Mendoza, Argentina. *Journal of Mammalogy* 72:194–198.
- MCKENNA, M. C., AND S. K. BELL. 1997. Classification of mammals above the species level. Columbia University Press, New York.
- MILLER, G. S., JR., AND J. W. GIDLEY. 1918. Synopsis of the supergeneric groups of rodents. *Journal of the Washington Academy of Sciences* 8:431–448.
- NEVO, E. 1999. Mosaic evolution of subterranean mammals: regression, progression, and global convergence. Oxford University Press, New York.
- PASCUAL, R., J. PISANO, AND E. J. ORTEGA. 1965. Un nuevo Octodontidae (Rodentia, Caviomorpha) de la Formación Epecuén (Plioceno medio) de Hidalgo (Provincia de La Pampa). Consideraciones sobre los Ctenomyinae Reig, 1958, y la morfología de sus molariformes. *Ameghiniana* 4:19–30.
- PEARSON, O. P. 1984. Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. *Journal of Zoology (London)* 202:225–237.
- PEARSON, O., ET AL. 1968. Estructura social, distribución espacial y composición por edades de una población de tuco-tucos (*Ctenomys talarum*). *Investigaciones Zoológicas Chilenas* 13: 47–80.
- PEARSON, O., AND H. A. LAGIGLIA. 1992. "Fuerte San Rafael": una localidad tipo ilusoria. *Revista del Museo de Historia Natural de San Rafael (Mendoza)* 12:35–43.
- PHILIPPI, R. A. 1869. Ueber einige Thiere von Mendoza. *Archiv für Naturgeschichte, Berlin* 1:38–51.
- PHILIPPI, R. A. 1896. Descripción de los mamíferos traídos del viaje de exploración a Tarapacá, hecho por orden del Gobierno en el verano de 1884 a 1885, por Federico Philippi. *Anales del Museo Nacional de Chile, 1st section. Zoolojía*, 24 pp. Santiago, Chile.
- PUIG, S., M. I. ROSI, M. I. CONA, V. G. ROIG, AND S. A. MONGE. 1999. Diet of a Piedmont population of *Ctenomys mendocinus* (Rodentia, Ctenomyidae): seasonal patterns and variations according sex and relative age. *Acta Theriologica* 44:15–27.
- PUIG, S., M. I. ROSI, F. VIDELA, AND V. G. ROIG. 1992. Estudio ecológico del roedor subterráneo *Ctenomys mendocinus* en la precordillera de Mendoza, Argentina: densidad poblacional y uso del espacio. *Revista Chilena de Historia Natural* 65:247–254.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics. The southern cone. University of Chicago Press, Illinois 2:1–430.
- REIG, O. A. 1958. Notas para una actualización del conocimiento de la fauna de la Formación Chapadmalal. I. Lista faunística preliminar. *Acta Geológica Lilloana* 2:241–253.
- REIG, O. A. 1989. Karyotypic repatterning as one triggering factor in cases of explosive speciation. Pp. 246–289 in *Evolutionary biology of transient unstable populations* (A. Fontdevila, ed.). Springer-Verlag, Berlin, Germany.
- REIG, O. A., C. BUSCH, M. O. ORTELLS, AND J. R. CONTRERAS. 1990. An overview of evolution, systematics, population biology, cytogenetics, molecular biology and speciation in *Ctenomys*. Pp. 71–96 in *Evolution of subterranean mammals at the organismal and molecular levels* (E. Nevo and O. A. Reig, eds.). *Progress in Clinical and Biological Research*, Wiley-Liss, New York 335:1–443.
- REIG, O. A., AND P. KIBLISKY. 1969. Chromosome multiformity in the genus *Ctenomys* (Rodentia, Octodontidae): a progress report. *Chromosoma (Berlin)* 28:211–244.
- REIG, O. A., A. I. MASSARINI, M. O. ORTELLS, M. A. BARROS, S. I. TIRANTI, AND F. J. DYZENCHAUZ. 1992. New karyotypes and C-banding patterns of the subterranean rodents of the genus *Ctenomys* (Caviomorpha, Octodontidae) from Argentina. *Mammalia* 56:603–623.
- ROIG, V. G. 1965. Elenco sistemático de los mamíferos y aves de la provincia de Mendoza y notas sobre su distribución geográfica. *Boletín de Estudios Geográficos* 12:175–222.
- ROIG, V. G., AND O. A. REIG. 1969. Precipitin test relationships among Argentinian species of the genus *Ctenomys* (Rodentia, Octodontidae). *Comparative Biochemistry and Physiology* 30: 665–672.
- ROSI, M. I. 1983. Notas sobre la ecología, distribución y sistemática de *Graomys griseoflavus griseoflavus* (Waterhouse,

- 1837) (Rodentia, Cricetidae) en la provincia de Mendoza. *Historia Natural* 3:161–167.
- ROSI, M. I., M. I. CONA, S. PUIG, F. VIDELA, AND V. G. ROIG. 1996a. Size and structure of burrow systems of the fossorial rodent *Ctenomys mendocinus* in the piedmont of Mendoza province, Argentina. *Zeitschrift für Säugetierkunde* 61:352–364.
- ROSI, M. I., M. I. CONA, AND V. G. ROIG. 2002. Estado actual del conocimiento del roedor fosorial *Ctenomys mendocinus* Philippi 1869 (Rodentia: Ctenomyidae). *Mastozoología Neotropical* 9:277–295.
- ROSI, M. I., M. I. CONA, F. VIDELA, S. PUIG, S. A. MONGE, AND V. G. ROIG. 2003. Diet selection by the fossorial rodent *Ctenomys mendocinus* inhabiting an environment with low food availability (Mendoza, Argentina). *Studies on Neotropical Fauna and Environment* 38:159–166.
- ROSI, M. I., M. I. CONA, F. VIDELA, S. PUIG, AND V. G. ROIG. 2000. Architecture of *Ctenomys mendocinus* (Rodentia) burrows from two habitats differing in abundance and complexity of vegetation. *Acta Theriologica* 45:491–505.
- ROSI, M. I., S. PUIG, F. VIDELA, M. I. CONA, AND V. G. ROIG. 1996b. Ciclo reproductivo y estructura etaria de *Ctenomys mendocinus* (Rodentia, Ctenomyidae) del Piedemonte de Mendoza, Argentina. *Ecología Austral* 6:87–93.
- ROSI, M. I., S. PUIG, F. VIDELA, L. MADOERY, AND V. G. ROIG. 1992a. Estudio ecológico del roedor subterráneo *Ctenomys mendocinus* en la precordillera de Mendoza, Argentina: ciclo reproductivo y estructura etaria. *Revista Chilena de Historia Natural* 65:221–233.
- ROSI, M. I., J. A. SCOLARO, AND F. VIDELA. 1992b. Distribución y relaciones sistémicas entre poblaciones del género *Ctenomys* (Rodentia, Ctenomyidae) de la provincia de Mendoza (Argentina). *Miscel-lània Zoológica* 16:207–222.
- ROVERETO, C. 1914. Los estratos araucanos y sus fósiles. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 25: 1–247.
- RUSCONI, C. 1931. Las especies fósiles del género *Ctenomys* con descripción de nuevas especies. *Anales de la Sociedad Científica Argentina* 112:129–142, 217–236.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85:1–350.
- SLAMOVITS, C. H., J. A. COOK, E. P. LESSA, AND M. S. ROSSI. 2001. Recurrent amplifications and deletions of satellite DNA accompanied chromosomal diversification in South American tuco-tucos (genus *Ctenomys*, Rodentia: Octodontidae): a phylogenetic approach. *Molecular Biology and Evolution* 18: 1708–1719.
- STEIN, B. R. 2000. Morphology of subterranean rodents. Pp. 19–61 in *Life underground: the biology of subterranean rodents* (E. A. Lacey, J. L. Patton, and G. N. Cameron, eds.). University of Chicago Press, Illinois.
- TATE, G. H. H. 1935. The taxonomy of the genera of Neotropical hystricoid rodents. *Bulletin of the American Museum of Natural History* 68:295–447.
- THOMAS, O. 1903. New species of *Oxymycterus*, *Thrichomys*, and *Ctenomys* from S. America. *Annals and Magazine of Natural History, Series 7*, 11:226–229.
- THOMAS, O. 1918. Two new tuco-tucos from Argentina. *Annals and Magazine of Natural History, Series 9*, 1:38–40.
- THOMAS, O. 1921a. On mammals from the Province of San Juan, western Argentina. *Annals and Magazine of Natural History, Series 9*, 8:214–221.
- THOMAS, O. 1921b. The tuco-tuco of San Juan, Argentina. *Annals and Magazine of Natural History, Series 9*, 7:523–524.
- THOMAS, O. 1927a. On a further collection of mammals made by Sr. E. Budin in Neuquen, Patagonia. *Annals and Magazine of Natural History, Series 9*, 19:650–658.
- THOMAS, O. 1927b. On further Patagonian mammals from Neuquen and the Rio Colorado collected by Señor E. Budin. *Annals and Magazine of Natural History, Series 9*, 20:199–205.
- THOMAS, O. 1929. The mammals of Señor Budin's Patagonian expedition, 1927–28. *Annals and Magazine of Natural History, Series 10*, 4:35–45.
- TORRES-MURA, J. C., M. L. LEMUS, AND L. C. CONTRERAS. 1989. Herbivorous specialization of the South American desert rodent *Tympanoctomys barrerae*. *Journal of Mammalogy* 70: 646–648.
- TORT, J., C. M. CAMPOS, AND C. E. BORGH. 2004. Herbivory by tuco-tucos (*Ctenomys mendocinus*) on shrubs in the upper limit of the Monte desert (Argentina). *Mammalia* 68:15–21.
- VITULLO, A. D., E. R. S. ROLDÁN, AND M. S. MERANI. 1988. On the morphology of spermatozoa of tuco-tucos, *Ctenomys* (Rodentia: Ctenomyidae): new data and its implications for the evolution of the genus. *Journal of Zoology (London)* 215:675–683.
- WEIR, B. J. 1974. The tuco-tuco and plains vizcacha. Pp. 113–130 in *The biology of hystricomorph rodents* (I. W. Rowlands and B. J. Weir, eds.). *Symposia of the Zoological Society of London*, 34. Academic Press, London, England.
- WOOD, A. E. 1955. A revised classification of the rodents. *Journal of Mammalogy* 36:165–187.
- WOODS, C. A. 1993. Suborder Hystricognathi. Pp. 771–806 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.

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