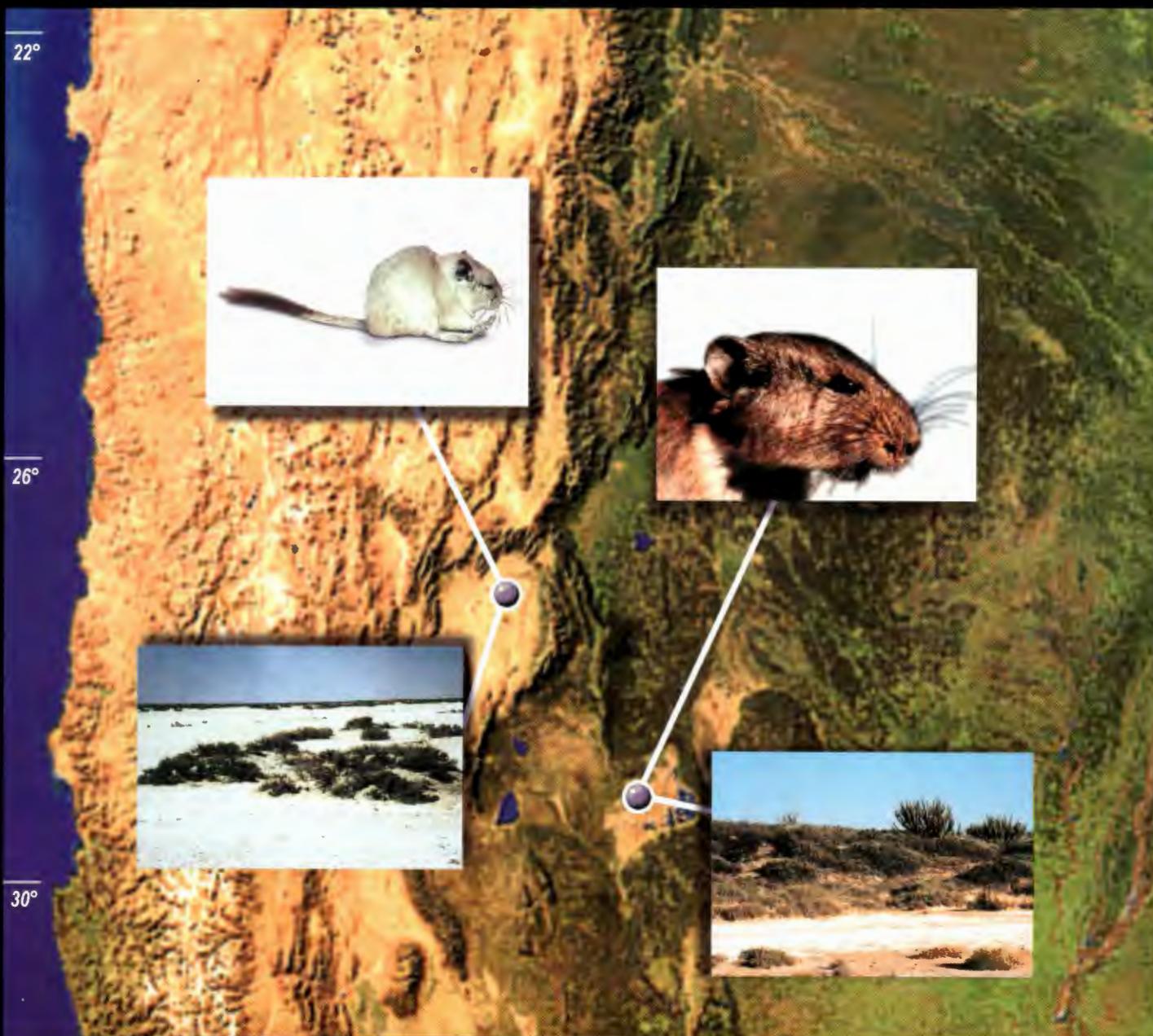


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**TWO NEW GENERA AND SPECIES OF HALOPHYTIC  
DESERT MAMMALS FROM ISOLATED SALT FLATS IN ARGENTINA**

## ABSTRACT

Two new genera and species of rodents are described from isolated salt pans in far northwestern Argentina. Both are members of the hystricognath family, Octodontidae. The two new genera are both specialized for life in zones of high salinity with halophytic vegetation growing at the periphery of saline flats. The new taxa are most closely related to *Tympanoctomys barrerae*, the Red Vizcacha Rat, which occurs in salt flats in central Argentina further to the south. One of the new mammals is restricted to an isolated salt flat lying within an enclosed bolsón in Catamarca Province. The other is limited to habitat islands that occur within the vast Salinas Grandes (great salt flat) of La Rioja Province in central Argentina. Taxonomic descriptions are included, as is information on relationships within the family Octodontidae. The biogeographic history of the group, and an evolutionary scenario for the evolution of the two new genera, are also discussed.

**Front cover:** The two new genera and their habitats are shown over a satellite composite photo of western Argentina. The isolated Bolsón de Pipanaco in the Monte Desert Biome is evident as the type locality for the Golden Vizcacha Rat. Both the rat and its habitat are shown in photos on the left side of the cover. The Chalchalero Vizcacha Rat occurs in the Salinas Grandes, a vast salt flat lying within the Chaco Biome. The position of the type locality for the rat is indicated. A photo of the new genus and species and its habitat are shown on the right side of the cover. Photos: M. A. Mares.

## TWO NEW GENERA AND SPECIES OF HALOPHYTIC DESERT MAMMALS FROM ISOLATED SALT FLATS IN ARGENTINA

MICHAEL A. MARES, JANET K. BRAUN, RUBÉN M. BARQUEZ, AND M. MÓNICA DÍAZ

South America is especially rich in mammals, with more than 1,000 species having been described to date (Patterson, 1994). Although the continental landmass makes up only 12 percent of the world total, 25 percent of the known species of mammals of the world occur in South America (Wilson and Reeder, 1993). In addition to supporting high levels of species richness on the continent as a whole, South America also has elevated species richness in particular localities ( $\alpha$  diversity). For example, sites in the lowland Amazon rain forest or on the rich moist forested slopes of the Peruvian Andes may support as many as 60 species of bats, along with 79 additional species of mammals (e.g., Patterson et al., 1998; Voss and Emmons, 1996). A pattern of changing mixes of species as one moves from the tropics to the temperate regions ( $\beta$  diversity) also contributes to the large numbers of mammal species found in South America (Mares and Ojeda, 1982).

There also are portions of the continent that support many endemic species, genera, and even families of mammals, and these sites are distributed differentially in the arid and semiarid parts of South America (Mares, 1992). Endemic and monotypic taxa contribute to elevated levels of higher-order genetic diversity that characterize the mammals of the continent's drier biomes. There has been some controversy about the idea of elevated diversity in arid lands (e.g., Mares, 1992; Voss and Emmons, 1996), but support for the idea of greater numbers of unique taxa or more threatened taxa in non-rain forest habitats extends to groups other than mammals (e.g., Barthlott et al., 1996, for flowering plants; Beissinger et al., 1996, for birds; Kalin Arroyo et al., 1988, for flowering plants; Mittermeier et al., 1999, for flowering plants; and Platnick, 1991, for spiders).

In recent years we have been surveying the mammals of Argentina. Because of a long history of sporadic collecting in the country (e.g., Crespo, 1960; Hershkovitz, 1987; Mares, 1982), and with most collecting having taken place in populated easternmost Ar-

gentina, many workers have considered the country to be well studied from the standpoint of its mammal fauna. However, we have encountered undescribed taxa of mammals in all parts of the country with some regularity. In recent years new taxa have been found in the mesic forests of the Northeast (e.g., Mares and Braun, 2000) and in the mesic Yungas forests of the Northwest (e.g., R. M. Barquez and M. M. Díaz, pers. obs.; M. A. Mares and J.K. Braun, pers. obs.). Most new taxa, however, have been encountered in the deserts, scrublands, and grasslands of western and northwestern Argentina (e.g., *Salinomys*—Braun and Mares, 1995; *Andalgalomys*—Mares and Braun, 1996; *Akodon aliquantulus*—Díaz et al., 1999).

Northwestern Argentina is interesting for a number of reasons. The entire zone consists of an integration of Andean and pre-Andean mountains and lowland desert valleys (Fig. 1). Some of the mountains are isolated from major mountain chains. The lowland desert valleys are also isolated from other similar valleys by the high mountains (e.g., Mares 1975, 1976; Mares et al., 1977; Mares et al., 1997; Morello, 1958; Orians and Solbrig, 1977; Williams and Mares, 1978). The region falls within the Tropical Andes designation as a biodiversity hotspot (Mittermeier et al., 1999), in part because of the verdant Yungas forest that extends along the eastern face of the easternmost mountains as far south as southern Catamarca Province (30° south latitude). The recognition of the region as a biological hotspot is also fitting because recent research suggests that the northern Monte Desert and its surrounding mountains are biologically distinct from the southern deserts. The biogeographic regions in far northwestern Argentina were once considered to be the Monte Desert in the lowland habitats (Morello, 1958) and the Puna and Prepuna deserts in the highlands (Cabrera, 1957, 1976). The topographically complex region is now viewed as different enough in its biological features that it has been suggested that it be recognized as a separate zoogeographic region: The Monte Desert of Mountains and Isolated Valleys (Burkart et al., 1999).

Presently, we are in the process of naming about a dozen taxa of previously undescribed mammals from northwestern Argentina; most have been collected only within the last few years. In this report, we describe two new genera and species of rodents from isolated salt flats in northern Argentina. These animals are especially unusual in that they are specialized for an existence in salt flats and forage on salt-adapted plants. Desert mammals specialized on the halophytic vegetation of salt flats are extremely rare. Worldwide, only three species of mammals (all rodents) are salt specialists: North American *Dipodomys microps*—the chisel-toothed kangaroo rat, family Heteromyidae (Kenagy, 1972); North African *Psammomys obesus*—the fat-tailed sand rat, family Muridae (Degan et al., 1988); and South American *Tympanoctomys barrerae*—the red vizcacha rat, family Octodontidae (Mares et al., 1997; Ojeda et al., 1999). Each species forages on halophytic vegetation and inhabits zones of high salt content, low plant diversity, high insolation, high temperatures, and low precipitation.

The new genera and species are in the family Octodontidae (tribe Octodontini) from the Monte Desert of Mountains and Isolated Valleys and the Dry Chaco. The family Octodontidae is known from the Late Oligocene in South America and the tribe Octodontini is known from the Late Miocene of Argentina (McKenna and Bell, 1997; Vucetich et al., 1999). One of the new taxa occurs in a valley (Fig. 1) that has been isolated from similar habitats by pre-Andean mountain ranges since their late Miocene-early Pliocene uplift (Pascual and Ortiz Jaureguizar, 1990). The other new taxon occurs in the Salinas Grandes (Great Salt Pan) of central Argentina (Fig. 1). The third known salt-specialist on the continent, *T. barrerae*, which is also an octodontid,

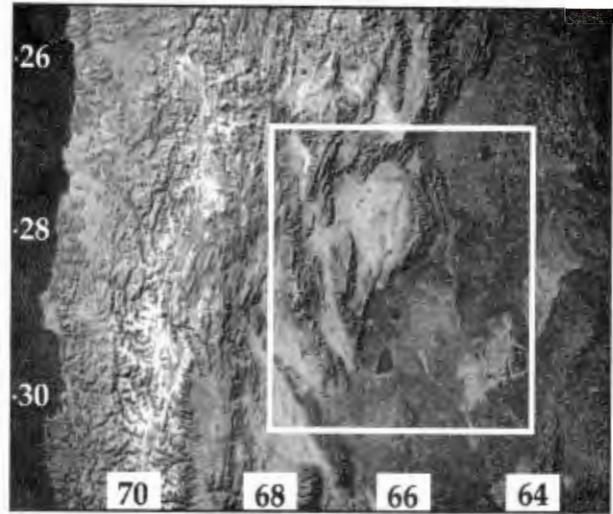


Figure 1. Satellite photo of arid western Argentina showing the isolated Bolsón de Pipanaco (enclosed in the square), as well as the Salinas Grandes (lower right in square). The high mountain ranges that demarcate the Monte, Puna, and Patagonian desert valleys are evident, with the pre-Andean ranges toward the east and the main Andean Cordillera to the west.

occurs in salt flats 600 km to the south (Mares et al., 1997; Ojeda et al., 1999).

Herein we describe two new genera and species and report the only known occurrence of three species of salt-specialized mammals from the same continent. Moreover, the discovery of two new monotypic genera of desert mammals continues to underscore the importance of arid South America as a major source of unique genetic diversity at supraspecific levels (Mares, 1992).

## MATERIALS AND METHODS

We took 19 external, cranial, dental, and mandibular measurements from specimens of the new taxa and from specimens of the other members of the family Octodontidae: *Aconaemys fuscus*, *Octodon bridgesi*, *O. degus*, *O. lunatus*, *Octodontomys gliroides*, *Octomys mimax*, *Spalacopus cyanus*, and *Tympanoctomys barrerae*. External measurements (in millimeters) from the labels were: total length, length from the tip of the snout to the last caudal vertebra;

length of head and body, total length less length of tail; length of tail, length of caudal vertebra; length of hind foot, length of pes from heel to tip of longest claw; length of ear, length of pinnae from notch.

Terminology for dentition generally follows Reig (1977). Cranial terminology generally follows Carleton and Musser (1989). Coloration of the holotypes follows those standards proposed by Ridgway (1912).

Cranial measurements (in millimeters) were taken with dial calipers to the nearest 0.1 mm and included: greatest length of skull, least distance from posterior border of supraoccipitals to tip of nasals; basal length, least distance from anterior edge of premaxillae to anteriormost point on lower border of foramen magnum; zygomatic breadth, greatest distance across zygomatic arches, perpendicular to longitudinal axis of cranium; mastoid breadth, greatest distance across the skull, including the mastoids; least interorbital breadth, least distance across frontal bones; length of nasals, greatest distance between margins of paired nasal bones from posteriormost projection of frontal suture to tip; breadth of rostrum, greatest width of rostrum across incisive capsules; length of diastema, distance between posterolateral margin of incisive alveolus and anteromedial margin of alveolus of P1; length of maxillary toothrow, distance from anterior margin of alveolus of P1 and posterior margin of alveolus of M3; length of bulla, greatest length of bulla; width of bulla, greatest width of bulla; width of zygomatic plate, width dorsal to insertion of zygomata on skull, parallel to longitudinal axis of skull; length of mandibular toothrow, distance from anterior margin of alveolus of p1 and posterior margin of alveolus of m3; length of mandible, distance between the median margin of alveolus of i1 and mandibular condyle.

Means, standard deviations, and ranges were calculated for adult specimens of each species. Unpaired

comparisons of the means (*t*-test) for each character for each species were performed using StatView (SAS Institute Inc., 1998). Means were considered statistically significant at  $P \leq 0.05$ . NTSYSpc (Numerical Taxonomy and Multivariate Analysis System, version 2.0; Rohlf, 1998) was used to generate a principal components analysis to evaluate the relationships among the taxa. Before ordination, characters were standardized (character means = 0, character variance = 1). Analyses were run using mean values for each taxon.

A series of 22 discrete-state characters was used for the cladistic analysis of the specimens listed in the Referred specimens and Appendix I. Values for the characters are given in Table 1. Character descriptions are given in Appendix II.

We used the Phylogenetic Analysis Using Parsimony program (PAUP 4.0 beta 2; Swofford, 1998) for parsimony analysis. The branch-and-bound algorithm was used, characters were unordered, zero-length branches were collapsed, the maximum number of minimum-length trees was set at 1000, and the simple addition sequence was selected. The branch-swapping algorithm used was tree bisection-reconnection. *Ctenomys* was used as the outgroup taxon based on studies that indicate that this genus (tribe Ctenomyini) is the sister group of the tribe Octodontini (Köhler et al., 2000; McKenna and Bell, 1997).

## RESULTS

### *Pipanacoctomys aureus* gen. et sp. nov.

*Type species*.—New species described herein.

*Included species*.—Only the type species.

*Holotype*.—Adult female; skin, skull, skeleton, and tissues; CML 6137 (Colección de Mamíferos Lillo, Universidad Nacional de Tucumán); collected 6 October 1998 by M. A. Mares, J. K. Braun, R. M. Barquez, and M. M. Díaz; field number Arg 4915.

*Referred specimens* (Paratypes).—Arg 4916, 4922, 4966, 5045, 5046, 5085.

*Type locality*.—Argentina: Catamarca Province: Departamento Pomán: 28 km S, 9.3 km W Andalgalá, 27° 50' 03" S, 66° 15' 50" W; elevation 680 m.

*Distribution*.—Known only from the type locality in Catamarca Province, Argentina (Figs. 2 and 3).

*Etymology*.—*Pipanaco*: for the Salar de Pipanaco (Pipanaco Salt Pan) in Catamarca Province, Argentina; *octo* (Latin): eight, referring to the cheek teeth, which are in the form of the numeral "8"; *mys* (Greek): mouse; *aureus* (Latin): gold, for the golden coloration. Common name: Golden Vizcacha Rat.

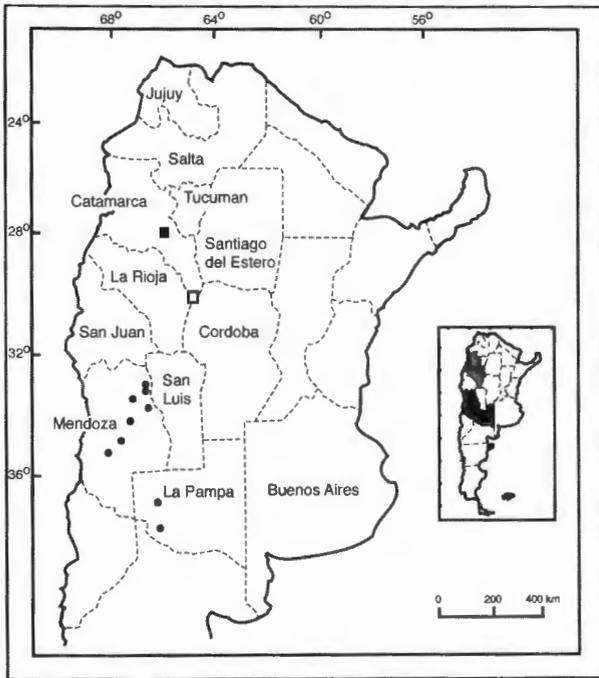


Figure 2. Map of northern Argentina showing localities for *Pipanacoctomys aureus* (closed square) and *Salinoctomys loschalchalerosorum* (open square). The localities for *Tympanoctomys barrerae* in Mendoza and La Pampa provinces are shown by closed circles.

**Diagnosis** (Figs. 4-6; Tables 1-4).—A member of the tribe Octodontini, subfamily Octodontinae, family Octodontidae. Size medium to large for the subfamily; pelage pale golden blond dorsally and white to pale creamy white ventrally; tail long, 76-85% head-body length, with well-developed rufous tuft; pinna about 12% head-body length; hind foot about 22% head-body length; bristle bundles present, but not well developed, and soft. The cranium differs from that of all other octodontids in having the following combination of characters: distinct groove and flange for infraorbital nerves; postorbital process or protuberance located on the frontal; palate long, extending beyond the posterior border of M2; paraoccipital process wide, flattened, and completely adpressed to the bulla; posterolateral border of the incisive foramen raised, which in lateral view appears as a protuberance anterior to P1; angle of suture between the jugal and zygomatic process of the maxillary sharply acute; interpremaxillary foramina small; bulla large and inflated; area anterior to bulla with two foramina, posterior opening of the alisphenoid canal and



Figure 3. Saline habitat of *Pipanacoctomys aureus* showing burrows placed under *Heterostachys ritteriana*. Sparse smaller shrubs are evident grading across the salty soil to the saline flat in the background.

foramen ovale (bony piece separating the two may be lost during specimen preparation); upper incisors light orange with narrow white lateral edge; and M3 with metacone and hypocone well developed forming a triangular-shaped posterior extension.

**Description.**—Size medium to large (Figs. 4-6; Tables 1-4), total length 298-318 mm; length of head and body 169-178 mm; length of tail 129-145 mm; length of hind foot 37-40 mm; length of ear 20-22 mm. General external characters as for the tribe. Tail long (76-85% head-body length), with pronounced tuft extending 35-40 mm beyond tip; tail well haired, scales not visible; pinna medium for subfamily (about 12% head-body length); pinna sparsely haired but outer and inner surfaces covered with fringe of whitish hairs; buccal bristles present, but not well developed, hairs soft; fore- and hind feet covered with whitish hairs; soles of hind foot naked with six well-developed plantar pads; hind foot with fringes of hairs medially and laterally (well developed); stiff bristle of hairs present above the claws of digits of hind foot.

Coloration of the holotype follows terms proposed by Ridgway (1912). Overall dorsal coloration pale blond (see cover photo and Fig. 4). Dorsal hairs (about 21 mm in length) are Neutral Gray basally (10 mm), followed by a band between Chamois and Cream-Buff, and a dark terminal tip (about 1 mm). Guard hairs (up



Figure 4. Photo of *Pipanacoctomys aureus*.

to 26 mm) are dark overall and are about the same color throughout their length. A distinct lateral line is absent, although the dorsal coloration grades gradually into the ventral coloration on the sides, which are therefore paler than the dorsum. Overall ventral coloration is whitish or pale cream. Hairs of the chest and throat lack gray bases. Hairs of the belly (about 11 mm) have a basal Pale Neutral Gray band (about 3 mm). Proximal one-third of tail bicolored, Clay above and Light Buff below. Distal two-thirds of tail between Cinnamon-Brown and Ochraceous-Tawny both above and below.

General cranial and dental characters as for the tribe. Skull (Fig. 5) medium in size; nasals short, not extending beyond fronto-premaxillary suture; nasal width gradually tapering posteriorly; tips of nasals about equal to gnathic process; interorbital region divergent, ledges and beading present; width of interorbital region greater than width of rostrum; zygomatic arches short and slightly convergent anteriorly; lacrimal small, well developed, and rounded; angle of fronto-parietal suture broadly acute or rounded; protuberance present at fronto-squamosal suture; protuberance present at squamosal-parietal suture; mastoid island large, length and width about 5.4 mm; area between mastoid islands broad, width > 8.5 mm; posterior border of interparietal nearly a straight line; hamular process of squamosal narrow.

In lateral view, the following characters are visible. Diastema steeply angled downward from incisor to premolar; posterolateral border of incisive foramen raised, which appears as a protuberance anterior to P1; infraorbital canal with distinct groove and flange for



Figure 5. Dorsal, ventral, and lateral view of the skull, lateral view of the mandible, and upper and lower left toothrows of *Pipanacoctomys aureus*.

the infraorbital ramus of the trigeminal nerve; angle of suture between jugal and zygomatic process of maxillary sharply acute; jugal thick, especially at suture between jugal and zygomatic process of maxillary; postglenoid fossa long and narrow.

Ventrally (Fig. 5), interpremaxillary foramen anterior to incisive foramina small and round or oval; pala-

tal process of premaxilla short and oblong, the midline raised, and separate from the palatal process of maxilla; pair of foramina present at posterior border within incisive foramina; palate long, extending beyond the posterior border of M2; palate with numerous small foramina and fragile, thin plates extending upward from the palate; midline of palate a raised thin plate; pair of posterior palatal foramina between P1 and M1; posterior margin of hard palate an inverted open "V" shape and without processes; small foramen posterior to M3; presphenoid and basisphenoid broad; pterygoid hamulus long, thick, and completely adpressed to auditory bulla; pterygoid with distinct groove laterally; auditory bulla large and inflated; foramen ovale and posterior opening of the alisphenoid canal located anterior to the bulla; paraoccipital process wide, flattened, and completely adpressed to bulla.

Upper incisors light orange with narrow white lateral edges; opisthodont; P1-M2 "8"-shaped, edges rounded; P1 slightly narrower in width than M1-M3; paracone, metacone, protocone, and hypocone of P1 about equal in size, metaflexus about equal to hypoflexus; metaflexus of P1 and M1 directed slightly posteriorly; paracone and metacone of M1 and M2 slightly smaller than protocone and hypocone, metaflexus shallower than hypoflexus; M1 and M2 about equal in width, size, and shape; paracone and protocone of M3 well developed, metacone and hypocone not equal in size to former, but with triangular-shaped posterior extension.

Lower incisors light orange, thin (width of single incisor, 1.35-1.4 mm); p1 slightly narrower than m1 and m2, shape of hypoconid and entoconid like that of m1 and m2, metaconid and protoconid and procingulum forming a triangle with a rounded apex, hypoflexid directed anteriorly and slightly larger than mesoflexid, metaconid with slight indentation; m1 and m2 "8"-shaped, major conids present, well developed, and about equal in size and shape with rounded edges, hypoflexid directed anteriorly; m3 "T" or "C"-shaped, protoconid and hypoconid present and well developed, entoflexid small or absent, entoconid small or absent, metaconid present or absent.

Angular (lunar) notch deep; coronoid process small; angular process of mandible thin and not flattened.

Thyrohyal bone of hyoid long and narrow; entoglossal process of hyoid small and narrow; atlas with large, thin ventral tubercle 2.5-3.0 mm in length, transverse process large and wing-like with two large foramina on each side, one foramen on each side of the neural arch; axis with neural spine large and extending posteriorly beyond third cervical vertebra; 13 ribs, the last very small; 28 caudal vertebrae.

*Habitat*.—The habitat (Fig. 3) consists of perisaline shrublands associated with the Salar de Pipanaco. Low (generally less than 1 m) chenopodiaceous shrubs (*Heterostachys* sp., *Atriplex lampa*, *Suaeda divaricata*) dominate the area and the substrate is mainly sand with significant amounts of salt. The animals are restricted to a narrow band of halophytic plant habitat that lies between the bare salt flat and the more typical Monte Desert habitats of *Prosopis*, *Larrea*, and the other perennial trees and shrubs of the Monte (Mares et al., 1985).

*Specimens examined* (7).—ARGENTINA: Catamarca Province: Departamento Pomán: Establecimiento Río Blanco, 28 km S, 9.3 km W Andalgalá, 27°50' S, 66°16' W; elevation 680 ± 61 m (holotype CML 6137, paratypes Arg 4916, 4922, 4966, 5045, 5046, 5085).

*Salinoctomys loschalchalersorum*  
gen. et sp. nov.

*Type species*.—New species described herein.

*Included species*.—Only the type species.

*Holotype*.—Adult male; skin, skull, skeleton, and tissues; CML 3695 (Colección de Mamíferos Lillo, Universidad Nacional de Tucumán); collected 25 July 2000 by M. A. Mares; field number Arg 5111.

*Referred specimens* (Paratype).—Arg 5121.

*Type locality*.—Argentina: La Rioja Province: Departamento Chamental: 26 km SW Quimilo, 30° 02' 43.4" S, 65° 31' 13.4" W; elevation 581 m.

*Distribution*.—Known only from the type locality in La Rioja Province, Argentina (Figs. 1, 2, and 7).

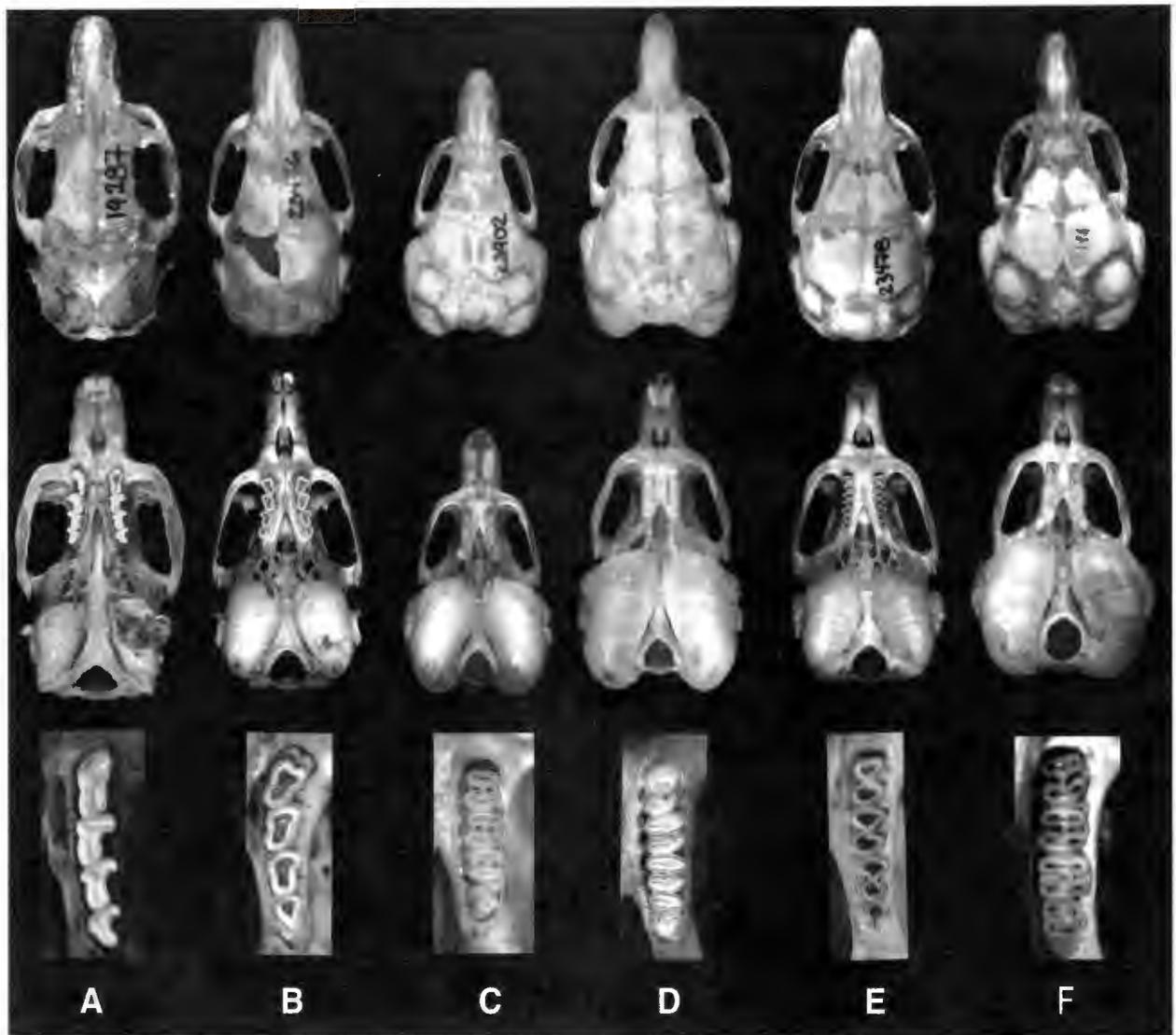


Figure 6. Dorsal and ventral views of the skulls and left upper tooththrow of: A) *Octodon degus*; B) *Octodontomys gliroides*; C) *Tympanoctomys barrerae*; D) *Pipanacoctomys aureus*, new species (holotype CML 6137); E) *Octomys mimax*; and F) *Salinoctomys loschalchalersorum*, new species (holotype CML 3695).

*Etymology*.—*Salin*: for the Salinas Grandes (Great Salt Pan) in La Rioja Province, Argentina; *octo* (Latin): eight, referring to the cheek teeth, which are in the form of the numeral “8”; *mys* (Greek): mouse; *loschalchalerosorum*: named for the great Argentine folklore group, “Los Chalchaleros,” in honor of their 52 years singing the traditional music of western Argentina, its habitats, and its history. Common name: Chalchalero Vizcacha Rat.

*Diagnosis* (Figs. 6, 8, and 9; Tables 1-4).—A member of the tribe Octodontini, subfamily Octodontinae, family Octodontidae. Size medium for the subfamily; pelage brownish black dorsally and white ventrally; tail long, 76-77% head-body length, with black tuft; pinnae about 11% head-body length; hind foot about 19% head-body length; bristle bundles present, but not well developed, hairs soft. The cranium differs from that of all other octodontids in having the following combination of characters: distinct groove and small flange for infraorbital nerves present; interpremaxillary foramen large; supraoccipital with distinct medial crest; palate short, extending to the middle of M2; paraoccipital process wide, flattened, and completely adpressed to the bulla; angle of suture between the jugal and zygomatic process of the maxillary sharply acute; distinct “knob” present posterior to suture between the jugal and zygomatic process of the maxillary; bulla large and inflated; posterior opening of the alisphenoid canal and foramen ovale present, the latter displaced posteriorly toward the bulla; foramen magnum with a distinct downward orientation; upper incisors light orange with narrow white lateral edge; and M3 with metacone and hypocone well developed laterally.

*Description*.—Size medium (Figs. 6, 8, and 9; Tables 1-4), total length 255, 275 mm; length of head and body 156, 144 mm; length of tail 119, 111 mm; length of hind foot 30, 28 mm; length of ear 17, 16 mm. General external characters as for the tribe. Tail long (76-77% head-body length), with tuft extending 20-25 mm beyond tip; tail well haired, scales not visible; pinnae small for subfamily (about 11% head-body length); pinna sparsely haired, with inner surfaces covered with fringe of whitish hairs and outer surfaces covered with whitish hairs with brownish tips; buccal bristles present, but not well developed, hairs soft; fore- and hind feet



Figure 7. Saline habitat of *Salinoctomys loschalchalerosorum*.

covered with whitish to pale brownish hairs; soles of hind feet naked with six well-developed plantar pads; hind feet with fringes of hairs medially and laterally (well developed); stiff bristle of hairs present above the claws of digits of hind feet.

Coloration of the holotype follows terms proposed by Ridgway (1912). Overall dorsal coloration between Drab and Hair Brown with Fuscous Black intermixed.

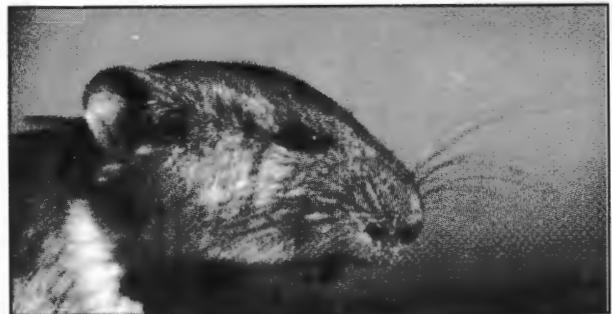


Figure 8. Photo of *Salinoctomys loschalchalerosorum*.

Dorsal hairs (about 20 mm in length) are Deep Neutral Gray basally (about 13 mm), followed by a band of Wood Brown (about 5 mm), and with a Fuscous Black tip (about 2 mm). Guard hairs (about 20 mm) are dark overall and are about the same color throughout their length. A lateral line is absent. Overall ventral coloration is white. Some scattered hairs of the chest and throat have Pale Neutral Gray bases. Hairs of the belly (about 10 mm) are white to the base on one specimen and have a basal light gray band in the second specimen. Proximal one-third to one-half of the tail is bicolored, Wood Brown to Fuscous Black above and whitish below. Distal one-half to two-thirds of tail Fuscous Black above and below.

General cranial and dental characters as for the tribe. Skull (Fig. 9) small to medium in size; nasals short, not extending beyond fronto-premaxillary suture; nasal width gradually tapering posteriorly; tips of nasals about equal to gnathic process; interorbital region divergent, ledges and beading present; width of interorbital region greater than width of rostrum; zygomatic arches short and only slightly convergent anteriorly; lacrimal small, well developed, and elongate; angle of fronto-parietal suture broadly acute or rounded; protuberance present at fronto-squamosal suture; protuberance present at squamosal-parietal suture; mastoid island large, length and width about 6.3 mm; area between mastoid islands narrow, <8.5 mm; posterior border of interparietal rounded; hamular process of squamosal narrow; supraoccipital with marked medial crest.

In lateral view, the following characters are visible. Diastema angled downward from incisor to pre-molar; infraorbital canal with distinct groove and small flange for the infraorbital ramus of the trigeminal nerve; angle of suture between jugal and zygomatic process of maxillary sharply acute; distinct “knob” present posterior to suture between the jugal and zygomatic process of the maxillary; jugal thick, especially at suture between jugal and zygomatic process of maxillary; postglenoid fossa long and narrow.

Ventrally (Fig. 9), interpremaxillary foramen anterior to incisive foramina large and oval; palatal process of premaxilla short and oblong, and separate from the palatal process of maxilla; pair of foramina located behind the posterior border of the incisive foramina; palate short, extending to the middle of M2; palate with numerous small foramina and thin plates extending upward from the palate; midline of palate raised from middle to M2 to posterior border of palate; pair of small posterior palatal foramina located about the middle of M2, either of which may be obsolete; posterior margin of hard palate an inverted open “V” shape and without processes; small foramen posterior to M3; presphenoid and basisphenoid broad; pterygoid hamulus short, thick, and incompletely adpressed to auditory bulla; auditory bulla large and inflated; area anterior to bulla with two foramina, posterior opening of the alisphenoid canal and foramen ovale, the latter displaced posteriorly toward the bulla; pterygoid with distinct groove laterally; paraoccipital process wide, flattened, and completely adpressed to bulla.



Figure 9. Dorsal, ventral, and lateral view of the skull, lateral view of the mandible, and upper and lower left tooththrows of *Salinoctomys loschalchalersorum*.

Upper incisors orange with narrow white lateral edges; opisthodont; P1-M3 “8”-shaped, edges rounded; P1 slightly narrower in width than M1-M3; paracone, metacone, protocone, and hypocone of P1 about equal in size, metaflexus about equal to hypoflexus; metaflexus of P1 directed slightly posteriorly; paracone and metacone of M1 and M2 slightly smaller than protocone and hypocone, metaflexus slightly shallower than

Table 1. Values of discrete-state characters for taxa examined. See Appendix II for descriptions and states of characters. Genera are listed alphabetically.

Taxa	Characters																					
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1	1	2	2	
<i>Aconaemys fuscus</i>	0	0	0	0	1	0	0	?	0	1	1	1	0	0	0	?	0	0	0	0	1	0
<i>Ctenomys mendocinus</i>	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0
<i>Octodon bridgesi</i>	1	0	0	0	0	0	0	0	0	1	1	1	0	0	?	?	?	?	1	0	0	1
<i>Octodon degus</i>	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0
<i>Octodon lunatus</i>	1	0	0	?	0	0	0	0	0	1	1	?	0	0	?	?	?	?	1	0	0	1
<i>Octodontomys gliroides</i>	2	1	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	1	0
<i>Octomys mimax</i>	2	0	0	0	0	0	0	0	1	1	0	0	2	0	0	1	0	1	0	0	1	1
<i>Pipanaoctomys aureus</i>	2	1	1	1	2	1	1	1	2	1	0	0	2	1	1	2	1	1	1	0	2	1
<i>Salinoctomys loschalchalersorum</i>	1	1	1	0	1	1	0	1	2	1	0	0	2	1	1	2	1	1	1	0	2	1
<i>Spalacopus cyanus</i>	0	0	0	0	0	0	0	?	0	0	2	0	0	0	0	?	0	1	0	2	0	1
<i>Tympanoctomys barrerae</i>	1	1	2	0	1	1	0	2	2	0	0	0	2	1	1	2	1	1	1	0	2	1

hypoflexus; M1 and M2 about equal in width, size, and shape; paracone and protocone of M3 well developed, metacone and hypocone slightly smaller than former.

Lower incisors orange and thin (width of single incisor, 1.5 mm); p1 slightly narrower than m1 and m2, shape of hypoconid and entoconid like that of m1 and m2, metaconid and protoconid and procingulum forming a triangle with a rounded apex, small anteroflexid present, hypoflexid directed anteriorly and about equal to mesoflexid, metaconid with slight indentation; m1 and m2 "8"-shaped, major conids present, well developed, and about equal in size and shape with rounded edges, hypoflexid directed anteriorly; hypoconid and entoconid of m2 smaller than protoconid and metaconid; m3 "C"-shaped, protoconid and hypoconid present and well developed, metaflexid small or absent, entoconid absent, metaconid present.

Angular (lunar) notch deep; coronoid process small; angular process of mandible thin and not flattened.

Thyrohyal bone of hyoid long and narrow; entoglossal process of hyoid a large, thick, well-developed knob; atlas with large, thin ventral tubercle 2.1 mm in length, transverse process large and wing-like with two large foramina on each side, two foramina located on each side of the neural arch, height of dorsal process less than that of transverse process; axis with

neural spine large, which extends posteriorly to just anterior of the third cervical vertebra; 13 ribs, the last very small; 25 caudal vertebrae.

*Habitat.*—The habitat consists of perisaline shrublands associated with the Salinas Grandes along the edges of thorn scrub islands that rise within the salt flat and provide dense thorn scrub on sandy substrate.

Plants associated with the burrows are generally less than 1 m in height, with the exception of tall cacti (*Cereus* sp.) and occasional trees, and include the chenopodiaceous shrub *Heterostachys ritteriana*, as well as the chenopodes (*Allenrolfea patagonica* and *Atriplex argentina*). Other plants on the site were *Monttea aphylla* (Scrophulariaceae), *Munroa argentina* (Gramineae), *Aphyllocladus spartioides* (Asteraceae), *Lycium tenuispinosum* and *Grabowskia boheraviaefolia* (Solanaceae), *Cortesia cuneifolia* (Boraginaceae), *Senna aphylla* (Fabaceae), *Agrostis pyramidalis* and *Setaria* sp. (Gramineae), *Alternanthera nodifera* (Amaranthaceae), and *Prosopis strombulifera* (Leguminosae). *Salinoctomys* is restricted to a narrow band of halophytic plant habitat that lies between the bare salt flat and the dense thorn scrub habitat of cacti, trees, and shrubs that is typical of the Gran Chaco (Mares et al., 1985). The most abundant plant in the immediate area of the burrow system is *Heterostachys ritteriana*.

*Specimens examined* (2).—ARGENTINA: La Rioja Province: Departamento Chamental: 26 km SW

Quimilo, 30° 02' 43.4" S, 65° 31' 13.4" W; elevation 581 m (holotype CML 3695, paratype Arg 5121).

### COMPARISONS

A comparison (Tables 1-4; Fig. 6) of *Pipanacoctomys* and *Salinoctomys* with other octodontid rodents follows. Both taxa differ from all other octodontid rodents in coloration. *Aconaemys* and *Spalacopus* have the following characteristics that distinguish them from *Pipanacoctomys* and *Salinoctomys*: tail short and untufted; bristle bundles absent; interorbital region narrow, less than width of rostrum; bulla small and uninflated; paraoccipital process small, thick, and fused incompletely to the bulla; angular (lunar) notch shallow; postglenoid fossa small and round; lacrimal large and triangular-shaped; metacones and hypocones not well developed; postorbital process absent (like *Salinoctomys*, but unlike *Pipanacoctomys*); paired foramina at the posterior border of the incisive foramina absent; raised lateral edges at the posterior border of the incisive foramina absent (like *Salinoctomys*, but unlike *Pipanacoctomys*).

*Aconaemys* is distinguished further by: upper incisors solid orange; and zygomatic arches parallel-sided.

*Spalacopus* further is distinguished by: dorsal coloration brownish black; ears greatly reduced; upper incisors white and proodont; zygomatic arches expanded; and distinct groove for infraorbital ramus of the trigeminal nerve in the infraorbital canal absent.

*Octodon* has the following characteristics that distinguish it from *Pipanacoctomys* and *Salinoctomys*: dorsal coloration brownish or grayish (like *Salinoctomys*, but unlike *Pipanacoctomys*); tail color is similar to that of the dorsum; tail with small tuft (like *Salinoctomys*, but unlike *Pipanacoctomys*); bristle bundles absent; upper incisors solid orange; zygomatic arches parallel-sided; interorbital region narrow; postorbital process present (like *Pipanacoctomys*, but unlike *Salinoctomys*); shape of suture of jugal and zygomatic process of squamosal squarish; lacrimal large and triangular; paired foramina at the posterior border of the incisive foramina absent; raised lateral edges at the posterior border of the incisive foramina absent (like

*Salinoctomys*, but unlike *Pipanacoctomys*); bulla small and uninflated; paraoccipital process small, thick, and fused incompletely to the bulla; postglenoid fossa small and round; area anterior to bulla with three foramina, posterior opening of the alisphenoid canal, foramen ovale, and middle lacerate foramina sometimes divided; molariform teeth crescent-shaped; metacones and hypocones not well developed; angular (lunar) notch shallow; angular process flattened.

*Octodontomys* has the following characteristics that distinguish it from *Pipanacoctomys* and *Salinoctomys*: dorsal coloration grayish brown; tail with a reddish buffy brush; bristle bundles absent; upper incisors solid orange; postorbital process absent or reduced (like *Salinoctomys*, but unlike *Pipanacoctomys*); interorbital region narrow, width about equal to the width of the rostrum; shape of suture of jugal and zygomatic process of squamosal squarish or rounded; lacrimal large and triangular; palate short, an inverted "V" shape, not extending beyond M1; paired foramina at the posterior border of the incisive foramina absent; raised lateral edges at the posterior border of the incisive foramina absent (like *Salinoctomys*, but unlike *Pipanacoctomys*); bulla medium and slightly inflated; paraoccipital process small, thick, and incompletely fused to the bulla; postglenoid fossa small and round; hamular process of squamosal well developed; two large foramina present, foramen ovale and posterior opening of the alisphenoid canal, middle lacerate foramina tiny; upper incisors orthodont; molariform teeth crescent-shaped; metacones and hypocones not well developed; angular (lunar) notch shallow; angular process short, slightly flattened.

*Octomys* has the following characteristics that distinguish it from *Pipanacoctomys* and *Salinoctomys*: dorsal coloration pale tan; tail with well-developed brush similar in color to that of the dorsum; bristle bundles absent; upper incisors solid orange; palate short, not extending beyond the posterior border of M1; paired foramina at the posterior border of the incisive foramina

Table 2. External and cranial measurements (in millimeters) for *Pipanacoctomys aureus*, and *Salinoctomys loschalchalersorum*. Included are mean, standard deviation, sample size, and range. Significant differences in means (*t*-test;  $P \leq 0.05$ ) are indicated as follows: <sup>a</sup>*Pipanacoctomys* vs. *Tympanoetomys*; <sup>b</sup>*Salinoctomys* vs. *Tympanoetomys*; <sup>c</sup>*Pipanacoctomys* vs. *Salinoctomys*.

Character	Taxa			
	<i>Pipanacoctomys aureus</i>		<i>Salinoctomys loschalchalersorum</i>	
	Holotype CML 6137	All adults	Holotype CML 3695	Paratype Arg 5121
Total length <sup>a, c</sup>	315	306 ± 12, 4 (293 – 318)	275	255
Length of head and body <sup>a, c</sup>	170	170 ± 5, 4 (166 – 178)	156	144
Length of tail <sup>c</sup>	145	135 ± 9, 4 (127 – 145)	119	111
Length of hind foot <sup>b, c</sup>	37	37 ± 3, 4 (32 – 40)	30	28
Length of ear <sup>a, c</sup>	22	20 ± 1, 4 (19 – 22)	17	16
Greatest length of skull <sup>a</sup>	43.1	42.6 ± 1.6, 3 (40.8 – 43.9)	39.2	
Basal length <sup>a</sup>	35.1	37.1 ± 2.7, 3 (35.1 – 40.2)	36.6	
Zygomatic breadth <sup>a, c</sup>	20.7	20.9 ± 0.7, 3 (20.3 – 21.6)	19.5	18.8
Mastoid breadth	23.6	22.3 ± 2.6, 3 (19.3 – 24.1)	20.1	
Least interorbital breadth <sup>a</sup>	9.0	8.9 ± 0.4, 3 (8.4 – 9.3)	8.4	7.5
Length of nasals <sup>c</sup>	13.7	13.8 ± 0.1, 3 (13.7 – 13.9)	14.2	14.0
Breadth of rostrum <sup>a, c</sup>	6.6	6.7 ± 0.1, 3 (6.6 – 6.8)	6.3	6.2
Length of diastema	8.8	8.7 ± 0.3, 3 (8.4 – 9.0)	7.9	8.2
Length of maxillary tooththrow <sup>a</sup>	6.7	7.1 ± 0.4, 3 (6.7 – 7.5)	6.4	5.5
Length of bulla <sup>a, c</sup>	19.2	19.2 ± 0.1, 3 (19.1 – 19.3)	18.0	17.0
Width of bulla	11.5	11.5 ± 0.3, 3 (11.2 – 11.8)	10.7	11.7
Width of zygomatic plate <sup>a</sup>	1.7	1.6 ± 0.1, 3 (1.5 – 1.7)	1.3	1.3
Length of mandibular tooththrow <sup>a</sup>	6.6	6.8 ± 0.2, 3 (6.6 – 7.1)	6.6	5.8
Length of mandible	21.2	21.5 ± 1.0, 3 (20.7 – 22.7)	20.6	19.8

absent; raised lateral edges at the posterior border of the incisive foramina absent (like *Salinoctomys*, but unlike *Pipanacoctomys*); postorbital process absent (like

*Salinoctomys*, but unlike *Pipanacoctomys*); suture of jugal and zygomatic process of squamosal squarish; paraoccipital process small and incompletely fused to

Table 3. External and cranial measurements (in millimeters) for *Tympanoctomys barrerae*, *Octomys mimax*, *Octodontomys gliroides*, and *Aconaemys fuscus*. Included are mean, standard deviation, sample size, and range. Significant differences in means (*t*-test;  $P \leq 0.05$ ) are indicated as follows: <sup>a</sup>*Pipanaoctomys* vs. *Tympanoctomys*; <sup>b</sup>*Salinoctomys* vs. *Tympanoctomys*.

Character	Taxa			
	<i>Tympanoctomys barrerae</i>	<i>Octomys mimax</i>	<i>Octodontomys gliroides</i>	<i>Aconaemys fuscus</i>
Total length <sup>a</sup>	262 ± 26, 8 (232 – 297)	369 ± 73, 13 (283 – 508)	324 ± 15, 29 (301 – 361)	259 ± 11, 2 (252 – 267)
Length of head and body <sup>a</sup>	145 ± 11, 8 (125 – 160)	212 ± 73, 13 (140 – 330)	176 ± 8.5, 29 (159 – 190)	180 ± 14, 2 (172 – 187)
Length of tail	118 ± 18, 8 (93 – 147)	157 ± 20, 13 (105 – 179)	149 ± 11, 29 (115 – 177)	63 ± 29, 3 (30 – 80)
Length of hind foot <sup>b</sup>	34 ± 2, 8 (30 – 36)	34.7 ± 1.3, 13 (32.3 – 36.6)	35.8 ± 1.6, 30 (31.4 – 39.0)	31 ± 9, 4 (18 – 37)
Length of ear <sup>a</sup>	16.3 ± 2.2, 8 (130 – 19.4)	24.1 ± 2.2, 13 (21.4 – 27.4)	28.2 ± 2.3, 30 (21.1 – 32.0)	20 ± 2, 3 (18 – 22)
Greatest length of skull <sup>a</sup>	37.9 ± 2.1, 3 (36.1 – 40.2)	43.7 ± 1.1, 9 (41.8 – 45.5)	45.3 ± 1.3, 25 (42.4 – 47.7)	43.2 ± 0.4, 2 (42.9 – 43.4)
Basal length <sup>a</sup>	27.8 ± 0.1, 2 (29.7 – 29.8)	37.2 ± 1.2, 8 (35.1 – 38.5)	39.6 ± 1.3, 22 (37.3 – 42.4)	38.6 ± 0.4, 2 (38.3 – 38.9)
Zygomatic breadth <sup>a</sup>	18.8 ± 0.7, 3 (18.1 – 19.3)	21.8 ± 0.6, 10 (20.8 – 22.6)	23.3 ± 0.7, 26 (22.0 – 24.4)	24.8 ± 0.3, 2 (24.6 – 25.0)
Mastoid breadth	22.3 ± 1.0, 3 (21.1 – 23.0)	21.6 ± 0.6, 8 (21.0 – 22.7)	22.1 ± 0.7, 21 (21.1 – 23.1)	18.3 ± 0.4, 2 (18.0 – 18.6)
Least interorbital breadth <sup>a</sup>	7.7 ± 0.6, 3 (7.1 – 8.2)	10.0 ± 0.6, 12 (9.1 – 11.2)	9.4 ± 0.4, 29 (8.6 – 10.2)	8.0 ± 0.2, 3 (7.9 – 8.2)
Length of nasals	11.3, 1	15.4 ± 0.6, 10 (1.1 – 16.4)	16.6 ± 0.9, 26 (13.0 – 17.5)	16.2 ± 1.2, 4 (15.1 – 18.0)
Breadth of rostrum <sup>a</sup>	6.3 ± 0.1, 2 (6.2 – 6.4)	7.6 ± 0.3, 11 (7.1 – 8.1)	8.2 ± 0.3, 26 (7.7 – 8.9)	9.0 ± 0.8, 4 (7.8 – 9.5)
Length of diastema	7.9 ± 0.5, 3 (7.5 – 8.5)	9.9 ± 0.6, 12 (8.7 – 10.9)	11.5 ± 0.5, 28 (10.7 – 12.5)	11.0 ± 1.2, 5 (9.7 – 12.5)
Length of maxillary toothrow <sup>a</sup>	5.9 ± 0.1, 4 (5.8 – 6.0)	8.1 ± 0.4, 9 (7.4 – 8.5)	8.1 ± 0.6, 28 (7.4 – 9.6)	8.5 ± 0.7, 5 (7.9 – 9.7)
Length of bulla <sup>a</sup>	17.2 ± 0.9, 3 (16.3 – 18.1)	15.8 ± 0.3, 9 (15.3 – 16.3)	14.6 ± 0.7, 23 (13.1 – 15.6)	11.1 ± 0.1, 2 (11.0 – 11.1)
Width of bulla	11.6 ± 0.2, 3 (11.4 – 11.7)	11.4 ± 0.3, 9 (10.9 – 11.8)	11.3 ± 0.3, 23 (10.7 – 11.9)	8.9 ± 0.1, 2 (8.8 – 9.0)
Width of zygomatic plate <sup>a</sup>	1.1 ± 0.2, 2 (0.9 – 1.2)	1.6 ± 0.1, 11 (1.5 – 1.8)	1.9 ± 0.2, 26 (1.3 – 2.3)	2.2 ± 0.3, 5 (1.8 – 2.5)
Length of mandibular toothrow <sup>a</sup>	6.0 ± 0.4, 3 (5.7 – 6.4)	8.2 ± 0.4, 8 (7.5 – 8.9)	8.5 ± 0.6, 27 (7.9 – 10.1)	9.5 ± 0.7, 5 (8.9 – 10.6)
Length of mandible	20.0 ± 0.6, 4 (19.1 – 20.6)	24.9 ± 0.8, 9 (23.8 – 25.9)	27.5 ± 0.9, 28 (26.0 – 29.5)	26.7 ± 1.7, 3 (24.8 – 28.1)

the bulla; postglenoid fossa small and round; two large foramina present, foramen ovale and posterior opening of the alisphenoid canal, middle lacerate foramina tiny;

molariform teeth angular “8”-shaped; metacones and hypocones not well developed; angular (lunar) notch shallow; angular process slightly flattened.

Table 4. External and cranial measurements (in millimeters) for *Octodon bridgesi*, *Octodon degus*, *Octodon lunatus*, and *Spalacopus cyanus*. Included are mean, standard deviation, sample size, and range.

Character	Taxa			
	<i>Octodon bridgesi</i>	<i>Octodon degus</i>	<i>Octodon lunatus</i>	<i>Spalacopus cyanus</i>
Total length	343 ± 24, 2 (325 - 359)	312 ± 23, 9 (272 - 341)	349 ± 23, 9 (318 - 398)	187 ± 18, 8 (147 - 203)
Length of head and body	191 ± 15, 2 (181 - 202)	181 ± 29, 9 (115 - 212)	195 ± 15, 9 (168 - 221)	138 ± 13, 8 (112 - 152)
Length of tail	151 ± 9, 2 (144 - 157)	130 ± 11, 9 (120 - 157)	153 ± 10, 9 (145 - 177)	50 ± 9, 8 (35 - 66)
Length of hind foot	38 ± 2, 4 (36 - 40)	36 ± 2, 9 (34 - 39)	37 ± 1, 9 (35 - 39)	29 ± 3, 9 (25 - 32)
Length of ear	25 ± 2, 4 (23 - 27)	28 ± 3, 7 (23 - 30)	28 ± 2, 8 (24 - 29)	11 ± 1, 9 (9 - 13)
Greatest length of skull	44.7 ± 2.6, 4 (40.9 - 46.7)	42.6 ± 2.0, 9 (39.8 - 46.5)	46.1 ± 1.4, 8 (44.3 - 48.2)	39.5 ± 2.7, 7 (36.9 - 44.2)
Basal length	39.2 ± 0.9, 4 (38.3 - 40.2)	36.4 ± 1.7, 9 (33.9 - 39.0)	32.3 ± 1.5, 8 (36.4 - 41.3)	35.6 ± 2.8, 7 (33.0 - 40.8)
Zygomatic breadth	24.2 ± 0.6, 3 (23.7 - 24.9)	22.8 ± 0.7, 9 (21.7 - 23.5)	24.5 ± .07, 7 (23.4 - 25.3)	23.4 ± 0.8, 6 (22.8 - 24.9)
Mastoid breadth	21.3 ± 0.3, 4 (21.0 - 21.7)	17.7 ± 3.3, 3 (13.9 - 20.1)	20.8 ± 0.2, 8 (20.5 - 21.1)	17.8 ± 1.2, 8 (16.5 - 19.4)
Least interorbital breadth	9.1 ± 0.6, 5 (8.5 - 9.9)	9.6 ± 0.4, 9 (9.1 - 10.2)	8.7 ± 0.3, 8 (8.1 - 9.1)	8.5 ± 0.5, 9 (7.9 - 9.5)
Length of nasals	17.6 ± 0.9, 4 (17.0 - 18.9)	15.9 ± 0.8, 9 (14.6 - 17.2)	17.9 ± 1.0, 7 (16.5 - 19.3)	13.2 ± 0.8, 7 (12.3 - 14.5)
Breadth of rostrum	8.3 ± 0.3, 5 (8.0 - 8.6)	7.5 ± 0.4, 9 (6.9 - 8.4)	7.9 ± 0.3, 8 (7.6 - 8.5)	7.5 ± 0.7, 6 (6.9 - 8.7)
Length of diastema	10.1 ± 0.5, 5 (9.5 - 10.6)	9.7 ± 0.6, 9 (9.1 - 10.9)	10.3 ± 0.8, 8 (8.7 - 11.2)	12.5 ± 1.0, 8 (11.7 - 14.4)
Length of maxillary toothrow	9.7 ± 0.5, 5 (9.0 - 10.4)	8.9 ± 0.6, 9 (8.2 - 10.0)	9.7 ± 0.4, 8 (9.2 - 10.2)	7.1 ± 0.6, 8 (6.5 - 8.2)
Length of bulla	13.3 ± 0.4, 4 (13.0 - 13.7)	12.9 ± 0.9, 9 (11.8 - 14.2)	13.9 ± 0.7, 8 (13.1 - 15.4)	10.8 ± 0.8, 8 (9.5 - 11.6)
Width of bulla	9.9 ± 0.3, 4 (9.5 - 10.1)	9.2 ± 0.4, 9 (8.6 - 9.7)	10.1 ± 0.2, 8 (9.9 - 10.5)	7.6 ± 0.4, 8 (7.2 - 8.5)
Width of zygomatic plate	1.9 ± 0.3, 4 (1.5 - 2.2)	1.6 ± 0.3, 9 (1.3 - 2.2)	1.5 ± 0.2, 8 (1.0 - 1.8)	1.2 ± 0.3, 9 (0.8 - 1.6)
Length of mandibular toothrow	10.0 ± 0.2, 4 (9.8 - 10.3)	9.3 ± 0.4, 9 (8.6 - 10.0)	9.9 ± 0.3, 8 (9.4 - 10.4)	7.7 ± 0.5, 8 (7.1 - 8.3)
Length of mandible	28.8 ± 0.4, 5 (28.3 - 29.3)	26.6 ± 1.2, 8 (24.5 - 27.9)	29.1 ± 1.1, 8 (27.1 - 30.6)	27.0 ± 1.6, 8 (25.6 - 30.3)

*Tympanoctomys* has the following characters that distinguish it from *Pipanaoctomys* and *Salinoctomys*: dorsal coloration tan washed with black (like *Salinoctomys*, but unlike *Pipanaoctomys*); tail with a short, black brush (like *Salinoctomys*, but unlike

*Pipanaoctomys*); bristle bundles well developed and hairs stiff; hairs of fringe on lateral edge of hind foot long and dense; ratio of length of hind foot to length of head and body > 23% (like *Pipanaoctomys*, > 21%; unlike *Salinoctomys*, < 19.5 %); raised lateral edges

at the posterior border of the incisive foramina absent (like *Salinoctomys*, but unlike *Pipanaoctomys*); posterior border of interparietal nearly a straight line (like *Pipanaoctomys*, but unlike *Salinoctomys*); supraoccipital with a medial crest (like *Pipanaoctomys*, but unlike *Salinoctomys* in which it is marked); foramen magnum with normal orientation (like *Pipanaoctomys*, unlike *Salinoctomys*); distinct groove for infraorbital ramus of the trigeminal nerve in the infraorbital canal absent; postorbital process absent (like *Salinoctomys*, but unlike *Pipanaoctomys*); shape of suture of jugal and zygomatic process of squamosal roundish or squarish; distinct “knob” absent posterior to suture between the jugal and zygomatic process of the maxillary (like *Pipanaoctomys*, unlike *Salinoctomys*); width between mastoid islands narrow (like *Pipanaoctomys*, unlike *Salinoctomys*); two large foramina present anterior to the auditory bullae, the foramen ovale and posterior opening of the alisphenoid canal present; pterygoid hamulus short, thin, and incompletely adpressed to bulla (like *Pipanaoctomys*, but unlike *Salinoctomys*); two foramina present on either side of the neural arch (like *Salinoctomys*, but unlike *Pipanaoctomys*).

*Salinoctomys* has the following characters that distinguish it from *Pipanaoctomys*: dorsal coloration tan washed with black; tail with a short black brush; postorbital process absent; lacrimal elongate; infraorbital canal small; interpremaxillary foramen large and oval; raised lateral edges at the posterior border of the incisive foramina absent; palate short; pterygoid hamular short, not completely adpressed to auditory bulla;

Table 5. Principal component loadings based on data for taxa examined. Relatively high loadings are denoted with an asterisk as follows: component I > 0.70; II > 0.70; III > 0.50.

Character	Principal Component		
	I	II	III
Total length	0.60	0.78*	0.05
Length of head and body	0.80*	0.43	0.08
Length of tail	0.32	0.92*	0.07
Length of hind foot	0.54	0.67	0.26
Length of ear	0.78*	0.51	0.10
Greatest length of skull	0.93*	0.28	-0.06
Basal length	0.56*	-0.11	-0.76*
Zygomatic breadth	0.88*	-0.43	0.06
Mastoid breadth	-0.12	0.83*	-0.10
Least interorbital breadth	0.63	0.36	-0.05
Length of nasals	0.93*	0.09	-0.04
Breadth of rostrum	0.86*	-0.37	-0.17
Length of diastema	0.56	-0.65	-0.07
Length of maxillary toothrow	0.96*	0.00	0.22
Length of bulla	-0.54	0.80*	-0.17
Width of bulla	-0.32	0.89*	-0.24
Width of zygomatic plate	0.76*	-0.04	-0.52*
Mandibular toothrow length	0.95*	-0.18	0.17
Length of mandible	0.90*	-0.32	0.20
Eigenvalues	9.90	5.57	1.19
Total variance (87.6%)	52.1%	29.3%	6.2%

foramen ovale smaller and displaced posteriorly near bulla; upper tooth row more divergent; two foramina present on each side of the neural arch of atlas.

## UNIVARIATE, MULTIVARIATE, AND PHYLOGENETIC ANALYSES

*Univariate analysis.*—The results of the unpaired comparisons of the means (*t*-test) for each character for *Pipanaoctomys*, *Salinoctomys*, and *Tympanoctomys* are presented in Tables 2 and 3. Means were considered to be statistically significant at  $P \leq 0.05$ . For *Pipanaoctomys* vs. *Tympanoctomys* the means for the following characters were significant: total length, length of head and body, length of ear, greatest length of skull, basal length, zygomatic breadth, least interorbital breadth, breadth of rostrum, length of max-

illary toothrow, length of bulla, width of zygomatic plate, and length of mandibular toothrow. For *Salinoctomys* vs. *Tympanoctomys* only the mean for length of the hind foot was significant, indicating that there is little size difference between the two taxa. For *Pipanaoctomys* vs. *Salinoctomys* the means for the following characters were significant: total length, length of head and body, length of tail, length of hind foot, length of ear, zygomatic breadth, length of nasals, breadth of rostrum, and length of bulla.

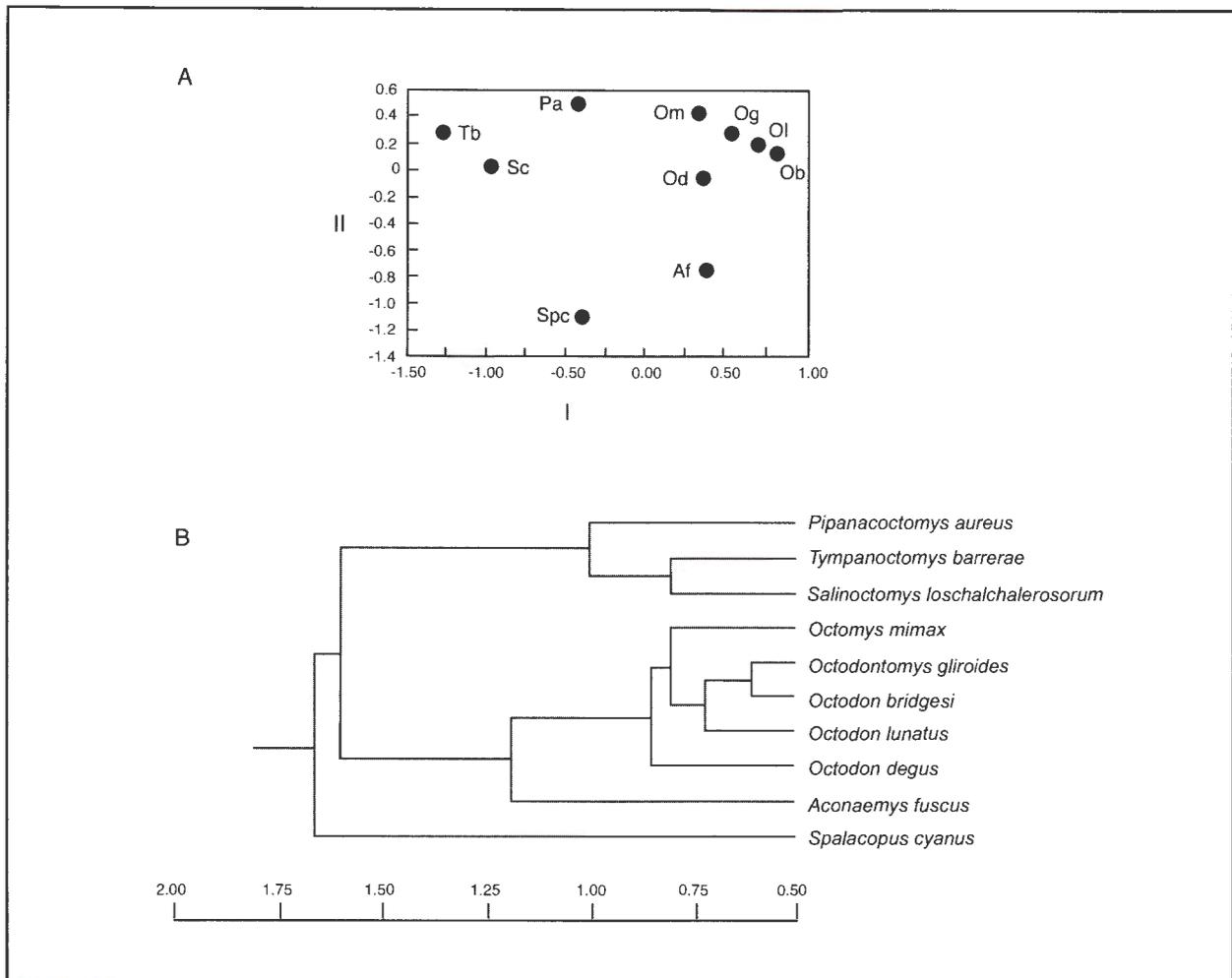


Figure 10. Multivariate relationships of species in the tribe Octodontini. A) Projections of scores for principal components I and II were extracted from correlations among 19 external and cranial measurements. Af = *Aconaemys fuscus*; Ob = *Octodon bridgesi*; Od = *Octodon degus*; Ol = *Octodon lunatus*; Og = *Octodontomys gliroides*; Om = *Octomys mimax*; Pa = *Pipanacoctomys aureus*; Sc = *Salinoctomys loschalchalersorum*; Spc = *Spalacopus cyanus*; Tb = *Tympanoctomys barrerae*. B) Phenogram (unweighted pair-group method using arithmetic averages) for taxa in the tribe Octodontini based on distance coefficients (cophenetic correlation coefficient = 0.84).

*Multivariate analysis.*—A principal components analysis of correlations among characters (Table 5) was used to evaluate the relationships among *Pipanacoctomys*, *Salinoctomys*, and other octodontid taxa. Eigenvalues for the first three principal components were 9.90, 5.57, and 1.19, respectively, explaining 87.6% of the total variance (52.1, 29.3, and 6.2%, respectively). About one-half (10 of 19) of the characters (Table 5) had high positive loadings on principal component I; this component may be related to size,

however, sample size is perhaps too small to make definitive conclusions. Component II separates taxa primarily by total length, length of tail, width of bulla, length of bulla, and mastoid breadth (loadings >0.70). Component III separated taxa primarily by basal length and width of zygomatic plate (loading >0.50).

In the bivariate plot of principal components I and II (Fig. 10A), *Pipanacoctomys* is placed between *Tympanoctomys* (and *Salinoctomys*) and *Octomys*. The

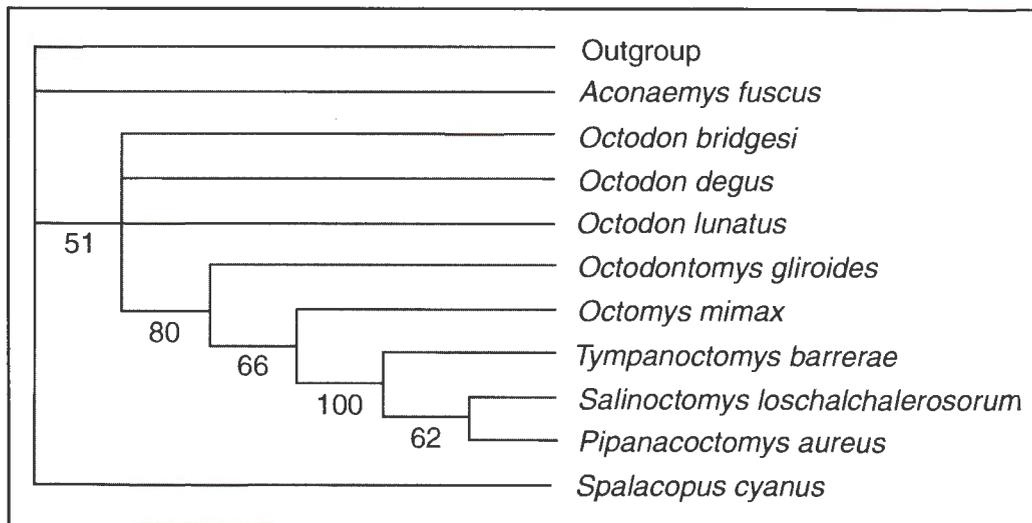


Figure 11. Cladogram of parsimony analysis of 22 characters for 10 octodontid taxa. *Ctenomys* is the outgroup. The tree shown is a bootstrap 50% majority-rule consensus (49 steps, CI = 0.653, RI = 0.730). Numbers appearing below the lines are bootstrap values.

three species of *Octodon* are clustered closely with *Octodontomys*. These taxa are placed in the upper half of the plot. *Aconaemys* and *Spalacopus* are located in the lower half of the plot.

A distance phenogram (Fig. 10B;  $r = 0.84$ ) shows several distinct clusters. *Pipanacoctomys*, *Salinoctomys*, and *Tympanoctomys* form a cluster distinct from the other octodontids, as does *Spalacopus*. The three species of *Octodon* are clustered with *Octomys* and *Octodontomys*. *Aconaemys* is distantly associated with this group.

*Phylogenetic analysis.*—A branch-and-bound search using all characters for all taxa resulted in eight

most parsimonious trees (46 steps). A bootstrap 50% majority-rule consensus tree (49 steps, CI=0.653, RI=0.730) is shown in Figure 11. The genera *Aconaemys* and *Spalacopus* are distinct lineages that are sister to the other members of the tribe. The relationship of the three species of *Octodon* is unresolved. Sister to the *Octodon* clade is the relatively well supported clade formed by the remaining octodontid taxa (*Octodontomys*, *Octomys*, *Pipanacoctomys*, *Tympanoctomys*, and *Salinoctomys*). In this clade, *Octodontomys* and *Octomys* are the most basal taxa. The clade formed by *Tympanoctomys* and *Salinoctomys* is well supported; *Pipanacoctomys* is the sister taxon to this clade.

## DISCUSSION

The discovery of two new genera and species of salt-specialized mammals might appear surprising given the rarity of this adaptive type in the deserts of the world, but it is less unexpected when the age and isolation of the region are considered. Argentina, particularly the Northwest, supports numerous extensive salt flats, many

lying within isolated valleys (see cover photo; Fig. 1) or separated from similar habitats by large areas of semi-arid thorn scrub or desert vegetation. *Pipanacoctomys aureus* is not the first new species described from the Bolsón de Pipanaco (Fig. 12). In 1972, Mares discovered and later described *Andalgalomys olrogi* (Will-

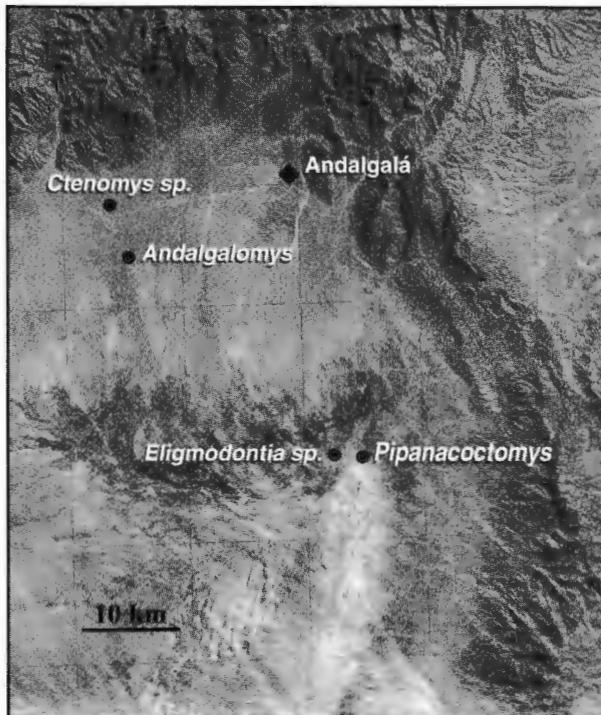


Figure 12. Aerial photo showing details of the northern Bolsón de Pipanaco, including type localities for four taxa in the northern part of the isolated valley and the town of Andalgalá. The high mountains forming the northeastern boundaries of the valley are evident.

iams and Mares, 1978), which is a species endemic to the valley. Mares also found an unnamed tuco-tuco (*Ctenomys* sp.) in 1971 that is also endemic to the valley. Recently we found a new species of gerbil mouse (*Eligmodontia* sp.) in the same valley that we are in the process of describing. We are learning that not only is this particular bolsón rich in new taxa, but the arid Northwest in general appears to harbor many new species of mammals in its numerous isolated valleys and mountains.

Similarly, *Salinoctomys loschalchalerosorum* is not the only new species we discovered on the habitat island rising from the immense Salinas Grandes (Fig. 13). We also found what appear to be as many as three new species of mammals in known genera. The salt flats of central Argentina are difficult habitats in which to work. For much of the year they are practically inac-

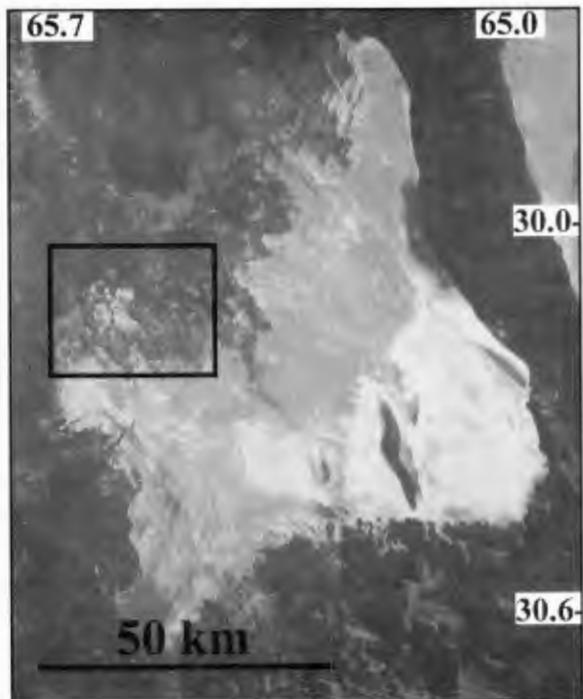


Figure 13. Aerial photo showing the placement of the Salinas Grandes, including the type locality for *Salinoctomys loschalchalerosorum* (box). The numerous habitat islands evident in the figure, even from a satellite, presumably will be found to support additional specimens of this new taxon.

cessible, becoming areas of deep, almost bottomless, salt mud that resists vehicular and even animal travel. In the dry, cool winter, when the saline areas are more accessible, the populations of mammals are in decline. We know of few other mammal surveying expeditions that have been made to these habitats. Given the fact that they have not been studied, that they are extensive, and that they are of great age and isolation, it is perhaps to be expected that we would have found some undescribed mammals.

The fact that the Northwest contains so many new taxa may result in part from the relatively recent orogeny of the region. In general, the series of Andean and pre-Andean mountain chains that rim the isolated valleys are fairly young, with most of the uplift having occurred since the Miocene. Indeed, significant uplift took place in the Pliocene or even as recently as the

Pleistocene (Pascual and Ortiz Jaureguizar, 1990). The mountains form barriers as high as 4,000 m that block prevailing winds from the east and lead to orographic rain falling on the eastern slopes of the eastern mountains, where the complex Yungas forest is found (Mares et al., 1996). As the uplifted wind currents drop their moisture and flow over the mountaintops, the lowlands to the west of these mountain chains receive warm, dry air.

Similarly, the massive Andes, whose peaks approach or exceed 7,000 m, also block any winds that might bring moisture from the west to the isolated valleys situated to the east. Unlike the basin and range topography of the American West, where mountain chains are generally aligned along a north-south axis, the pre-Andean chains may have long axes that are oriented from east to west or north to south. The result is that in extreme northwestern Argentina a series of isolated desert valleys has been formed. The mountains themselves may be isolated one from the other so that, like the valleys, the mountains become zones for speciation. Since the mountains are largely arid or semiarid, the result is that the biogeographic region called The Monte Desert of Mountains and Isolated Valleys is composed of a series of xeric islands at both high and low elevations—an ideal region for isolation and allopatric differentiation. The designation of the new biogeographic region thus reflects the unique geographical history of the area, and our data support the singular nature of the zone.

In effect, the region is a land-locked, topographically rich, terrestrial archipelago of habitat and tectonic islands that are themselves relictual mountains and valleys (Figs. 1 and 12). Mammals that may have colonized the region before the period of uplift would be expected to have had their geographic ranges broken into numerous populations that would diversify over time. The discovery of new monotypic genera in and adjacent to the region supports this hypothesis of biogeography and speciation.

We recognize that one of the new genera, *Salinoctomys*, was found within the great salt flat of central Argentina in the Chaco Domain and outside the strict limits of the proposed biogeographic region. However, the type locality is only 125 km distant from the mountains included in the bolson-montane biogeo-

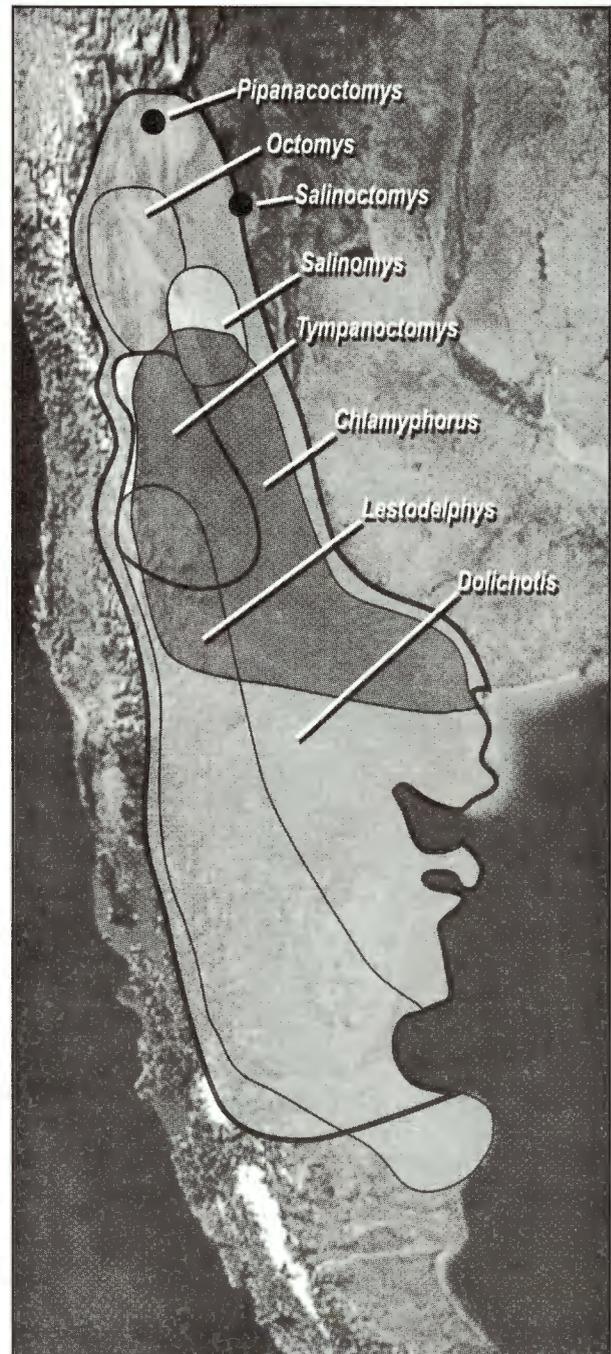


Figure 14. Satellite photo of arid western Argentina. The high mountain ranges that demarcate the Monte, Puna, and Patagonian desert valleys are evident, with the pre-Andean ranges toward the east and the main Andean Cordillera to the west. Shown are geographic ranges of eight endemic genera.

graphic region and the mammals of both areas shared a recent history. Our data suggest that some consideration should be given to including the isolated salt flats that rim the proposed new biogeographic region within the region. One must at least recognize the close association between some faunal elements associated with the salt flats and those of the isolated desert valleys and mountains lying slightly to the north and west.

Octodontids are of great age (McKenna and Bell, 1997; Vucetich et al., 1999) and show remarkable chromosomal variation, including a species that has among the highest number of chromosomes known for a mammal (102 in *Tympanoctomys barrerae*; Contreras et al. 1990)—the only known tetraploid mammal, Gallardo et al., 1999). Whether or not either of the new species is a tetraploid has not yet been determined.

Phylogenetic analysis of cranial and dental morphology (Fig. 11) and molecular data (R. J. Baker and F. Hoffmann, pers. comm.) suggest that *Pipanaoctomys*, *Salinoctomys*, and *Tympanoctomys* shared a common ancestor not shared by any other octodontid genera. The range of the putative ancestor was fractured by the uplifting pre-Andean chains resulting in the eventual formation of two monotypic genera, one being *Pipanaoctomys* and the other being the common ancestor of *Tympanoctomys* and *Salinoctomys*. Eventually, this ancestral population was divided into a northern and southern group as the huge salt flat of the Pliocene was divided into two major salt flats through climate change and habitat disruption. This hypothesis is supported by geological evidence that indicates that prior to the end of the Pliocene a single large basin existed in northwestern Argentina (Bailey et al., 1977; Periano, 1957). Two separate inland seas (Pascual and Jaureguizar, 1990; Vuilleumier, 1971) were found in the region: one in the far Northwest (where *Salinoctomys* and *Pipanaoctomys* occur today, and one in the south near Mendoza (where *Tympanoctomys* is found today). As these seas retreated due to changing climates and orographic uplift, the modern salt pans were formed. Associated with the salt flats that became increasingly isolated were the ancestors of today's salt-specialized octodontids.

*Tympanoctomys* forages on saltbush (*Atriplex*) in southern Mendoza, although it also consumes *Heterostachys* in some parts of its range (Torres-Mura

et al., 1989). Each of the three genera possesses the remarkable morphological structures (tooth-like brushes) that are used by *Tympanoctomys* to strip the saltbush leaves of their protective salt covering (Mares et al., 1997). *Pipanaoctomys*, which inhabits complex mounds at the edge of the salt pan, forages on *Heterostachys Ritteriana*. The plant has compressed leaves that form small, salt-filled balls. The high salt content of the *Heterostachys* leaves cannot be reduced via mechanical means (as can the leaves of *Atriplex*) and the buccal brushes of *Pipanaoctomys* seem to be less well-developed than those of *Tympanoctomys*. In feeding trials, *Pipanaoctomys* refused to eat saltbush (*Atriplex*) and another species of chenopodiaceous halophyte (*Suaeda*), both of which grow near the mounds, although in much lower frequency than *Heterostachys*. *Salinoctomys* seems to forage mainly on *Heterostachys* and grass, both of which were found in abundance in food stores in the burrows (pers. obs.). Its buccal brushes are more similar to *Pipanaoctomys* than they are to *Tympanoctomys*. Unfortunately, we have been unable to capture *Salinoctomys* alive to determine how they handle different food items while feeding.

*Tympanoctomys*, *Salinoctomys*, and *Pipanaoctomys* show pronounced philopatry to the salt pan habitat (pers. obs.). Given such unusual habitat requirements, ancestral populations would have been unlikely to have dispersed over mountain massifs or across hundreds of kilometers of non-saline habitat after isolation ensued. Gene exchange would thus have been extremely unlikely and this would explain how the ancestral populations diverged sufficiently to be recognized as distinct genera after 2 million years.

Recently, a monotypic genus of murid rodent (*Salinomys delicatus*) also was described from woodlands associated with salt pans in the Monte Desert to the south of the Bolsón de Pipanaco (Braun and Mares, 1995) and to the southeast of the Salinas Grandes. *Salinomys*, in a significant range extension, was found to co-occur with *Salinoctomys*, thus providing a site where two of the rarest mammals in the world occur together. Interestingly, the arid lands of Argentina comprise about 2.1 million km<sup>2</sup> (Roig et al., 1992) and support eight endemic genera of mammals (Fig. 14; *Lestodelphys*, *Chlamyphorus*, *Salinomys*, *Octomys*, *Pipanaoctomys*, *Salinoctomys*, *Tympanoctomys*, and *Dolichotis*; Wilson and Reeder, 1993; this paper). By

comparison, the entire conterminous United States (7.8 million km<sup>2</sup>) has only six endemic genera of mammals (*Microdipodops*, *Ochrotomys*, *Podomys*, *Arborimus*, *Neofiber*, and *Brachylagus*; Wilson and Ruff, 1999).

These results have relevance to the value of arid lands as important sources of species, genera, and even families of mammals when compared to the better-known Amazonian lowlands (Mares, 1992). The levels

of endemism and higher order genetic diversity evidenced by arid land mammals of South America appear to have resulted in part from the extensive geographic isolation present in southern regions of the continent. Due to the resulting mosaic of relictual mountains, valleys and saline flats—arid habitats requiring extensive levels of specialization at all levels of organization, from cells to populations—a series of unique, monotypic genera developed.

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## APPENDIX I

### Specimens examined

All specimens that were examined are listed along with localities and catalog numbers. All specimens are preserved as standard preparations of skin, skull, and skeleton and are housed in the: British Museum of Natural History, London (BM); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM); Colección de Mamíferos Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina (CML); Colección Mastozoológica, Instituto Argentina de Investigaciones de las Zonas Áridas, Mendoza, Argentina (IADZA-CM); Michigan State University Museum, East Lansing (MSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Sam Noble Oklahoma Museum of Natural History, Norman (OMNH); Museum of Texas Tech University, Lubbock (TTU). Field numbers of specimens in the Sam Noble Oklahoma Museum of Natural History and not yet cataloged are designated Arg.

*Aconaemys fuscus* (14).—ARGENTINA: Neuquén: Lago Correntoso (N. end), 1 (159433 MVZ); Lago Correntoso (N. end) (Ruca Malén), 2 (159431, 159434 MVZ). CHILE: Curico: Nr. Peteroa (Valle de las Cuevas, E side of Andes, nr. Volc. of Peteroa, alt. 6,000 ft.), 1 (55.12.24.195 BM). Malleco: 27 km W Angul in Parque Nacional, 3,800 ft., 2 (6347, 6348 MSU); Parque Nacional, 27 km WNW Angul, 3,650 ft., 1 (6346 MSU); Laguna Malleco, 25 km N Cunacautin, 3,000 ft., 1 (6349 MSU); Osorno: Puesto Montt, 1 (16.11.14.4 BM). Valdivia: vic. Valdivia, 1

(142176 MVZ). Chili, 3 (43.12.30.32, 56.7.1.1, 56.7.1.3 BM). No locality: 1 (no number BM).

*Ctenomys mendocinus* (7).—ARGENTINA: San Juan: 17 km ESE José Martí (by road) on road to Chañar Seco, 1 (3352 Arg); Quebrada de las Flores, 4 km E and 5 km N Guayamas, 1 (3406 Arg). San Luis: Gran Bajo Salitroso, 1 (3342 Arg) 6 km W Hualtaran, Parque Provincial Sierra de las Quijadas, 1 (3279 Arg); 8 km W of La Botija, Pampa de las Salinas, 1 (3240 Arg); 15 km E Salinas del Bebedero, 1 (544 Arg); Salinas del Bebedero, 15 km SE, 1 (3313 Arg).

*Octodon bridgesi* (7).—CHILE: Colchagua: Teno River, 2 (43.7.20.5, 55.12.24.196 BM). Malleco: 4 km W Baños Río Blanco, 3,200 ft., 1 (6345 MSU). Valparaíso: Quilpué, 150 m, 3 (9.6.13.2, 10.7.23.4, 10.7.23.5 BM). Chili, 1 (7.1.1.170 BM).

*Octodon degus* (26).—CHILE: Aconcagua: 3 km N Las Molles, 1 (28634 TTU). Atacama: 40 km E Vallenar, 2 (28636, 28637 TTU). Coquimbo: Fray Jorge, 1,000 ft., 1 (118664 MVZ); Fray Jorge Natl. Park, 5 (28635, 28638, 28639, 28640, 30232 TTU); 15 km S La Serena, 2 (28641, 28642 TTU). Santiago: Fundo Santa Laura, 8 km W Tilttil, 1,100 m, 1 (150076 MVZ); Fundo Santa Laura, approx. 10 km W Tilttil, 1,100 m, 2 (150072, 150075 MVZ); Fundo Santa Laura, Cuesta la Dormida, 8 km W of Tilttil, 1,000 m, 2 (150078, 150079 MVZ); Puente Alto, 800 m, 1 (4.1.7.13 BM);

Rinconada de Maipu, 5 (28643-28647 TTU). Valparaiso: Llinllin, Limache, 250 m, 1 (12183 CM); Olmué, 1 (12182 CM); Quilpué, 1 (2107 MSU). Chile, 1 (53.8.29.14 BM).

*Octodon lunatus* (12).—CHILE: Santiago: Fundo Santa Laura, 10 km W of Tilttil, 1100 m, 3 (150090, 150091, 150092 MVZ); Fundo Santa Laura, Cuesta la Dormida, 10 km W of Tilttil, 1000 m, 8 (150093, 150098, 150099, 150100, 150101, 150102, 150103 MVZ, 28633 TTU); Fundo Santa Laura, Cuesta la Dormida, 10 km W of Tilttil, 1100 m, 1 (150088 MVZ).

*Octodontomys gliroides* (32).—ARGENTINA: Jujuy: Alfarcito, 2600 m, 3 (21.11.1.74, 21.11.1.76, 21.11.1.78 BM); Casalindo, 4000 m, 2 (19.8.2.26, 19.8.2.27 BM); Cerro Casalindo, 4500 m, 1 (19.8.2.28 BM); 11 km east of Humahuaca, 2 km east of Pucará on road to Cianzo, 2 (23476 OMNH, 4477 IADIZA-CM); Maimara, 2230 m, 2 (12.12.12.42, 12.12.12.43 BM); Maimara, 2300 m, 2 (4917, 5007 CM); Maimara, 2600 m, 1 (12.12.12.44 BM); 10 km west of Puramarca on highway 52, 1 (3437 CML). Salta: Inca Mayo, 2500 m, 1 (34.11.4.94 BM); M. Sola, 2500 m, 8 (34.11.4.86-34.11.4.93 BM). BOLIVIA: Lipez, 4500 m, 1 (26.6.12.81 BM); Oruro, 3700 m, 2 (2.2.2.5, 2.2.2.7 BM); Potosi, 4400 m, 1 (2.2.2.2 BM); Est. Yuruma, 2200 m, 3 (26.6.12.76, 26.6.12.77, 26.6.12.80 BM); Yuruma, 2200 m, 1 (26.6.12.78 BM); Yuruma, 20 mi. SSE Tupiza, 10,500 ft., 1 (120236 MVZ).

*Octomys mimax* (17).—ARGENTINA: Catamarca: Puntilla, Tinogasta, 1000 m, 5 (20.5.11.29-20.5.11.33 BM). San Juan: Pedernal, 4,040 ft., 1 (23478 OMNH); Pedernal, 1200 m, 3 (21.6.19.11-21.6.19.13 BM); Parque Provincial Ishigualasto, 3 km N from headquarters, 1 (IADIZA-CM 4479); just inside Valle de la Luna, 5 (44068-44072 CM). San Luis: 6 km W Hualtaran, Parque Provincial Sierra de la Quijadas, 2,800 ft., 2 (Arg 3262, 3271).

*Spalacopus cyanus* (24).—CHILE: Aconcagua: 3 km N La Molles, 1 (28648 TTU). Coquimbo: Fray Jorge Park, 2 (28649, 28650 TTU); Las Plumas, 95 km N Los Vilos, 1 (28651 TTU). Santiago: Cerro Roble, 3 km NW Caleu, 2000 m, 1 (150111 MVZ); Cerro Roble, approx. 2 km S by rd. from summit, 3 km NW of Caleu, 2000 m, 2 (150110, 150112 MVZ); La Parva, 2700 m, 3 (28652-28654 TTU); La Parva, 3200 m, 1 (28655 TTU). Valparaiso: Quilpué, 1 (2108 MSU); Quilpué, 200 m, 1 (8.4.7.29 BM); Valparaiso, coast hills, 500 m, 8 (0.3.5.2-0.5.4.6, 1.3.21.14, 97.5.1.11, 98.1.8.5 BM). Chile, 1 (43.7.20.4 BM). S. Chile, 1 (73.12.16.4 BM). No locality, 1 (502.a BM).

*Tympanoctomys barrerae* (8).—ARGENTINA: Mendoza: 27 km N Desaguadero, 1,670 ft., 2 (3438 CML, 23477 OMNH); 40 km al N Desaguadero, camino a Arroyito, 1 (2747 IADIZA-CM); 16 km S, 3 km E Nihuil, 5 (3745 CML; 5346 IADIZA-CM; 23902 OMNH; 3789, 3797 Arg).

## APPENDIX II

## Descriptions of discrete-character states

Descriptions of discrete-character states and character state values are listed. Character states are given by numbers in parentheses and are in order (Table 1).

	External			10	Infraorbital canal: (0) No distinct groove and flange for infraorbital nerves. (1) Distinct groove and flange present.
1	Tip of tail: (0) Not pencilled. (1) Pencil small. (2) Pencil large.			11	Zygomatic arches: (0) Convergent anteriorly. (1) Parallel-sided. (2) Expanded.
2	Tail color: (0) Similar or somewhat similar to dorsum. (1) Different from dorsum.			12	Lacrimals: (0) Small. (1) Large.
3	Bristle bundles: (0) Absent. (1) Present, but not well developed. (2) Present, well developed.			13	Bullae: (0) Small and not inflated. (1) Medium and slightly inflated. (2) Large and inflated.
	Cranial			14	Foramina posterior to incisive foramina: (0) Absent. (1) One pair present.
4	Postorbital processes: (0) Absent. (1) Present.			15	Postglenoid fossae: (0) Small and round. (1) Large and narrow.
5	Length of palate: (0) Short, not extending beyond the posterior border of M1. (1) Short, extending to mid-M2. (2) Long, extending at least to the posterior border of M2.			16	Angular process: (0) Flattened. (1) Slightly flattened. (2) Thin, not flattened.
6	Paraoccipital processes: (0) Not adressed to bullae. (1) Adressed to bullae.			17	Angular (lunar) notch: (0) Shallow. (1) Deep.
7	Incisive foramina: (0) Edges not raised. (1) Edges raised.			18	Interorbital width: (0) Narrow, less than width of rostrum. (1) Wide, greater than width of rostrum.
					Dental
8	Suture between jugal and zygomatic process of squamosal: (0) Angle squarish. (1) Angle acute. (2) Angle roundish.			19	M3: (0) Metacone and hypocone not well developed. (1) Metacone and hypocone moderately to well developed.
9	Foramina anterior to bullae: (0) Posterior opening of alisphenoid canal, foramen ovale, and middle lacerate foramina present. (1) Posterior opening of alisphenoid canal and foramen ovale present; middle lacerate foramina tiny. (2) Posterior opening of alisphenoid canal and foramen ovale present.			20	Incisor position: (0) Opisthodont. (1) Orthodont. (2) Proodont.
				21	Incisor color: (0) White. (1) Orange. (2) Orange with lateral white edge.
				22	Molar shape: (0) Not "8"-shaped. (1) "8"-shaped.

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## PUBLICATIONS OF THE MUSEUM OF TEXAS TECH UNIVERSITY

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