

Pappogeomys tylorhinus.

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Pappogeomys tylorhinus (Merriam, 1895)

Tuza llanera

Platygeomys tylorhinus Merriam, 1895:167. Type locality "Tula, 6800 ft., Hidalgo."

Pappogeomys tylorhinus Russell, 1968:739. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Geomyidae, Subfamily Geomyinae, Genus *Pappogeomys*, Subgenus *Cratogeomys*. The genus *Pappogeomys* contains nine species. Six subspecies of *P. tylorhinus* (Russell, 1968) are recognized as follows:

P. t. angustirostris (Merriam, 1903:81). Type locality "Patamban, Michoacan, Mexico."

P. t. atratus (Russell, 1953:539). Type locality "top of Cerro Viejo de Cuyutlán, 9700 ft., 19 mi. S, 9 mi. W Guadalajara, Jalisco, México."

P. t. brevirostris Russell, 1968:733. Type locality "2 mi. E Celaya, 5800 ft., Guanajuato."

P. t. planiceps (Merriam, 1895:168). Type locality "north slope Volcán de Toluca, 9000 ft., México."

P. t. tylorhinus (Merriam, 1895:167). Type locality "Tula, 6800 ft., Hidalgo."

P. t. zodiuss (Russell, 1953:540). Type locality "13 mi. S 15 mi. W Guadalajara, about 4500 ft., Jalisco, México."

DIAGNOSIS. The pelage is soft and lax. It is similar to *P. gymnurus*, but smaller, with shorter and more hairy hind feet, which are distinctly white in contrast to the dark ankles and legs; the skull is broad and flat, as in *P. gymnurus*, but lighter and "differing further in important characters" (Merriam, 1895:167). The length of the skull is moderate for the *gymnurus* group. The condylobasal length of the skull varies from 50.4 to 58.3 mm in females and from 56.5 to 65.0 mm in males. The breadth across the squamosal bones usually equals or exceeds the breadth across the zygomatic arches (except in *P. t. zodiuss* and some specimens of *P. t. brevirostris*). The length of the rostrum is from 20.0 to 26.7 mm. Breadth of the squamosal bones for six subspecies average 63.4-71.7% of the condylobasal length (Russell, 1968).

GENERAL CHARACTERS. The tail of the tuza llanera averages 36-41% of length of head and body and is nearly naked (Fig. 1; Merriam, 1895). The ears are round and small. The upper parts of the body vary from pale ochraceous-buff to glossy black; the underparts are similar, slightly paler but never black in melanistic individuals, and with plumbeous showing through in places. The throat is gray or buffy, the legs and ankles are similar in color with the rest of the body, and the hind feet are whitish or brownish (Russell, 1968). The four large incisors remain outside the mouth when the mouth is shut. External cheek pouches are well developed. The front feet bear large and strong claws (Sosa, 1981).

External measurements (mm) of the type specimen (male adult) are: total length, 345; length of tail, 100; length of hind foot, 45. Average measurements for two females from the type locality were: total length, 298; length of tail, 91.5; length of hind foot, 39.5. Averages and ranges (in parentheses) of 22 adult females from the northern Valley of México are: total length, 302 (271-350); length of tail, 102 (80-115); and length of hind foot, 40 (35-45); the same measurements for 15 adult males from the same locality are: 336 (308-361); 112 (97-123); and 43 (40-49), respectively (Sosa, 1981). The mean total length (mm) and body mass (g) of 55 adult tuza llaneras from northern Mexico City are: males, 329.6 and 459.3, respectively; females, 280.7 and 387.2, respectively. Sex ratio was 1:1.14 in favor of females (Villa-C. and Sosa, 1984).

Cranial measurements (mm) of the type specimen are: greatest basal length, 61.5; basal length, 58; basilar length, 54.5; zygomatic breadth, 43; greatest breadth across squamosals, 44; breadth of postglenoid notch, 31; interorbital breadth, 8; greatest height of cranium above palate, 23.5; greatest height of cranium above inferior lip of foramen magnum, 18.5; length of upper molar series, 12; length of diastema, 24.5; greatest length of single half of mandible, 42; greatest breadth of mandible across angular processes, 52; distance from condyle to angular process, 18.5; breadth of muzzle at root of zygoma, 12.5; zygomatic breadth, 88.6; greatest squamosal breadth, 69.9; greatest height of cranium above palate, 38.2 (Merriam, 1895). Mean and range (in parentheses) for cranial measurements of 29 females from northern México City are: condylobasal length, 55.6 (51.0-61.0); zygomatic breadth, 38.1 (33.3-41.6); cranial height, 22.0 (20.0-23.9); length of palatal, 34.4 (31.2-37.7); length of nasals, 18.5 (16.0-21.5); breadth of cranium, 28.8 (26.4-31.3); squamosal breadth, 39.1 (34.6-43.4); rostrum width, 11.4 (9.9-13.7); length of rostrum, 22.4 (19.0-26.9); alveolar length, 13.1 (11.8-15.5). The same measurements for 17 males from the same localities (respectively) are: 60.2 (56.1-63.1); 42.3 (38.6-45.6); 23.7 (22.1-25.9); 37.6 (33.5-39.7); 20.7 (18.3-22.8); 30.8 (28.0-32.8); 43.3 (36.4-46.2); 12.0 (11.2-12.7); 24.7 (22.7-26.6); 13.8 (13.0-14.7—Sosa, 1981).

DISTRIBUTION. Tuza llanera is endemic to Central México and occurs in a disjunct pattern (Fig. 2). The species is found as far north as the state of Guanajuato and west to the states of Jalisco and Michoacan. In the eastern part of its distribution, *P. tylorhinus* ranges from the state of Hidalgo to southern Distrito Federal. The southernmost subspecies occur in the central valleys of Toluca and México (Berry and Baker, 1972; Hall, 1981; Russell, 1968).

FOSSIL RECORD. *Cratogeomys* (= *Pappogeomys*) *tylorhinus* was recorded from geological beds of upper "Becerra," in "Valle de Tequiquiac," State of Mexico (Hibbard, 1955). Remains of this species were found in Holocene sediments of the cave La Nopalera, in southwestern Hidalgo (Alvarez, 1964).

FORM AND FUNCTION. The skull is strongly platycephalic (although variation exists), indicating membership in the *gymnurus* species-group and distinctly separating *P. tylorhinus* from the *P. castanops* species group (Fig. 3). Platycephalic specializations include a flat, broad cranium, especially expanded posteriorly to the squamosal roots of the zygomatic arches, widely spreading rami of the lower jaws and elongated angular processes, and the rugosity



FIG. 1. An adult male tuza llanera (*Pappogeomys tylorhinus*).

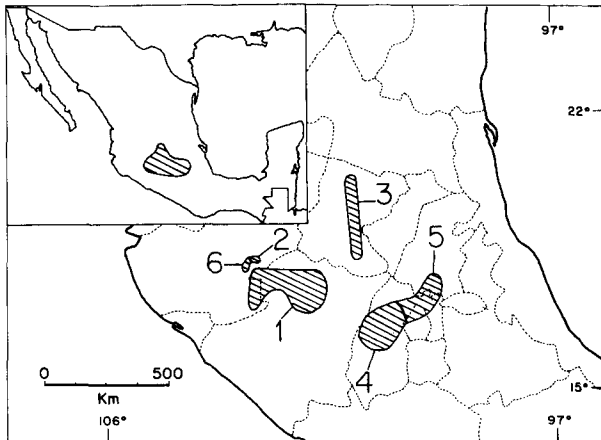


FIG. 2. Geographical distribution of the tuza llanera (*Pappogeomys tylorhinus*; after Hall, 1981). 1. *P. t. angustirostris*, 2. *P. t. atratus*, 3. *P. t. brevirostris*, 4. *P. t. planiceps*, 5. *P. t. tylorhinus*, 6. *P. t. zodiuss*.

and angularity of the occiput, including the lambdoidal crest and enlarged paraoccipital processes (Russell, 1968).

The skull of tuza llanera differs from that of *P. gymnurus* in its smaller size, narrower rostrum, and shorter nasals, which do not reach the plane of the zygomatic arches (Merriam, 1895). The most conspicuous difference is the shape of the nasals; instead of being wedge-shaped, as in *P. gymnurus*, they are much broader posteriorly and abruptly truncated behind, and the premaxilla do not approximate behind them. The skull of *P. tylorhinus* is less massive and the maxillary arm of the zygoma is thinner than in *P. gymnurus*. The jugal is enlarged throughout and expanded anteriorly into a broad plate which abuts against the sides of the maxillary part of the zygoma arch. The suture at the base of the maxillary root of the zygoma is broadly convex inward; in *P. gymnurus* it is shaped like a drawn out "S." As usual in geomyids, the skull of the female is much smaller than that of the male and the jugal is narrower. The dental formula is 1/1, 0/0, 1/1, 3/3, total 20 (Merriam, 1895).

Females do not have a vaginal sinus, each uterus joining the vagina independently, and placental scars are not recognizable. For nonpregnant mature females the length of each uterus varies from 14.8 mm to 31.0 mm and the width varies from 2.3 mm to 4.2 mm. Lactating females displayed just 3, 4, or 5 active mammae at once (Sosa, 1981).

The baculum is wide, dorsoventrally flattened, and gradually slender toward the tip (Burt, 1960); the tip is laterally expanded and flattened. Males do not have a defined scrotum, rather the testes are contained in a skin fold to the sides of the penis and the anus. Testes of adults and subadults are ovoid and range from 5.2 to 14.0 mm in length and from 4.5 to 10.4 mm in width. Body mass is positively and significantly correlated with testis length and testis width (Sosa, 1981).

Testes of reproductively active males are highly vascularized. The anterior part of the epididymis joins the testis whereas the posterior part is long and pendant and remarkably visible externally when the testes are inside the scrotum. The epididymis is thin and resembles the deferens duct, which is wrapped by mesenterium and leads along with the testicular vein to a short urogenital sinus. The testes, epididymides, and vas deferens are covered by a fat body, except in males with scrotal testes (Sosa, 1981).

The vas deferens meet at about the same level where the ureters join the urinary bladder. The reproductive accessory glands, except Cowper's glands, also join the reproductive ducts at this level. The seminal glands are tubular with lobes larger distally than proximally. These glands are translucent and produce a sticky, transparent secretion. Reproductive males have glands as long as 24 mm. The prostate consists of small, transparent lobes distally enlarged dorsolaterally to the urogenital sinus. Cowper's glands are solid, rounded bodies up to 5 mm in diameter and are located at the base of the penis (Sosa, 1981).

ONTOGENY AND REPRODUCTION. A pregnant female from northern Valley of México, collected in September, was



FIG. 3. Dorsal, ventral, and lateral views of cranium, and lateral and dorsal view of mandible of a male *Pappogeomys tylorhinus* from Pueblo Nuevo, state of México (Instituto de Biología, Universidad Nacional Autónoma de México, 10081). Greatest length of skull is 60.8 mm.

lactating. The head-rump length of the single fetus was 50 mm, with discoidal placentation (López-Forment, 1968). Other pregnant females were collected in July ($n = 1$), November ($n = 2$), and December ($n = 1$). The size of the embryo in July was 18.4 mm long by 5.1 mm wide; in November, both embryos were 7.0 mm in diameter and others were 6.5, 7.7, and 7.8 mm in diameter; and in December two embryos were 21.8 mm long by 6.8 mm wide and 20.3 mm long by 6.7 mm wide. The average litter size was two, usually with one fetus in each uterus. Females ovulate throughout the year (Sosa, 1981).

Males with scrotal or inguinal testes and epididymides full of sperm were found in July, September, and October. Two weaned juveniles (70.1 g and 67.5 g body mass) were recorded in September. The breeding season ranges from June to December (Sosa, 1981), but tuza llaneras from northern México City are reproductively active all year with a peak in December. Testis size does not necessarily indicate spermatogenesis and scrotal testes do not indicate sexual activity (Villa-C. and Sosa, 1984).

ECOLOGY. The tuza llanera is common along the north slope of the mountains around Lake Patzcuaro, Michoacán, and then NE to the vicinity of Lake Cuitzeo; their habitat is the zone immediately below the pine (*Pinus*) zone (from about 1,533 to 1,840 m in altitude), where fields of wheat and corn are largely grown. Tuza llanera is abundant in such fields, and cause considerable damage to the crops (Merriam, 1895). They also range up into the lower border of the pine forest where *Zygoeomys trichopus* is also found. The climate is cool with abundant rain during summer. In the Valley of Tula, Hidalgo, *P. tylorhinus* are found in small numbers at about 1,672 m, near Tula. They were only noted near the borders of small basin-like sinks where the land was under cultivation. This area is arid and warm (Merriam, 1895). Tuza llanera is a pest in northern Mexico City because of damage produced on crops in fields. *P. tylorhinus* also thrives in deforested lands (Villa-C. and Sosa, 1984), and occurs in grasslands and temperate forests of the western Valley of México, México, usually in sandy soils (Ceballos and Galindo, 1984).

Tuzas llaneras feed on native plants such as *Distichlis spicata*, *Crotalaria* sp., *Astragalus* sp., *Oenothera rosea*, *Verbena* sp., fruits of *Lepidium virginicum*, stems and leaves of *Alternanthera repens*, and roots of *Baccharis* sp. However, *P. tylorhinus* also eats the non-native weeds *Brassica campestris*, *Taraxacum officinale*, *Physalis* sp., *Dalea* sp., *Amaranthus* sp., *Eruca sativa*, *Lesquerella* sp., *Chenopodium* sp., and roots of *Bidens pilosa*, *Euphorbia prostata*, and *Xantocephalum centauroides* (López-Forment, 1968; Sosa, 1981).

The tuza llanera damages cultivated plants such as (in order of importance by extent of damage done by the gophers): alfalfa (*Medicago sativa*), maize (*Zea mays*), barley (*Hordeum sativum*), wheat (*Triticum vulgare*), and pumpkin (*Cucurbita pepo*). Damaged cultivated crops of lesser importance were romeritos (*Atriplex muricata*), tomato (*Lycopersicon esculentum*), lettuce (*Lactuca sativa*), coriander (*Coriandrum sativum*), parsley (*Petroselinum crispum*), and artichoke (*Cynara scolymus*). *P. tylorhinus* also causes significant economic losses to maguey (*Agave* aff. *atrovirens*), bean (*Phaseolus*), sweet bean (*Vicia faba*), pumpkin (*Cucurbita mexicana*), capulin (*Prunus capuli*), apple (*Pyrus malus*), pear (*Pyrus communis*), peach (*Prunus persica*), and apricot (*Prunus armenica*; López-Forment, 1968; Sosa, 1981).

Captive tuzas llaneras eat large amounts of alfalfa, carrots, lettuce, potatoes, peanut, corn, and jicama tubers (*Pachyrhizus erosus*). They also accept spinach, apples, and sorghum in lesser extent. These items were provided in the laboratory in the following proportions: 52% fresh green stems and leaves, 40% succulent roots, and 8% seeds. The daily amount of food taken varied from 60 to 65 g wet weight (Sosa, 1981). Tuzas llaneras refused to eat nopales (*Opuntia* stems), an abundant cultivated cactus in its habitat (López-Forment, 1968).

Nest material found in burrows of *P. tylorhinus* included entire plants of maize, salt grass (*Distichlis spicata*), and Bermuda grass (*Cynodon dactylon*), leaves and fruits of pirú tree (*Schinus molle*), roots and leaves of maguey, dry flowers of gordolobo (*Gnaphalium* sp.), and leaves of *Oenothera* sp., *Andropogon* sp. and capulin. Feathers, pieces of paper and plastic were also found (López-Forment, 1968).

Fauna commonly found in burrows of *P. tylorhinus* includes spiders (Araneidae), sun spiders (Solpugida), centipedes (Chilopoda), ticks and mites (Acarina), springtails (Collembola), pseudoscorpions (Pseudoscorpionida), *Ceuthophilus* crickets (Orthoptera), carabid beetles (Coleoptera), cicadas (Homoptera), woodlice (Isopoda), flies (Diptera), thrips (Thysanoptera), stoneflies (Psocoptera), salamanders (*Rhyacosirodon altamirani* and *Ambystoma tigrinum*), toads (*Spea hammondi*), snakes (*Toluca lineata*), lizards (*Sceloporus spinosus*), and long-tailed weasels (*Mustela frenata*). A pseudoscorpion was also collected from the pelage of a tuza llanera (López-Forment, 1968; Sosa, 1981).

Domestic dogs (*Canis familiaris*) and cats (*Felis catus*) actively prey on tuzas llaneras in the northern Valley of México. Suspected predators of tuzas llaneras include the gopher snake (*Pituophis deppei*), the barn owl (*Tyto alba*), hawks (*Buteo jamaicensis* and *Circus cyaneus*), the badger (*Taxidea taxus*), the long-tailed weasel (*Mustela frenata*), and the coyote (*Canis latrans*; López-Forment, 1968; Sosa, 1981).

The tuza llanera harbors the following ectoparasites (Barrera, 1961; López-Forment, 1968; Sosa, 1981): mites, Laelapidae (*Hirstionyssus femoralis*); ticks, Ixodidae (*Ixodes dampfi*); lice, Tri-

chodectidae (*Geomydoecus perotensis*, *G. geomyidis*, *G. polydentatus*, and *G. werneckii*); and fleas, Ceratophyllidae (*Dactylopsylla*?). Lice were the most abundant ectoparasites, particularly *G. polydentatus*, which occurred in densities of 6.4 lice/cm² on the head and anterior dorsal part of the body, 2.8 lice/cm² the dorsal lumbar region and the ventral part of the body, and 0.5 lice/cm² the forelimbs and hindlimbs. A female tuza llanera harbored a total of 1,187 lice (Sosa, 1981).

The following intestinal parasites have been found in tuzas llaneras: flatworms, Anoplocephalidae (two species of *Anoplocephaloides*) and the roundworms *Globicephala mexicanus* (Strongylidae). The roundworms *Skriabinoflaria* sp. (Filariidae) and *Litomosoides carini* (Onchocercidae) were collected from the thoracic and abdominal cavities (González, 1984; López-Forment, 1968; Sosa, 1981).

BEHAVIOR. The tuza llanera is territorial, solitary, and fossorial (Sosa, 1981). The sexes only meet to breed. Individuals live inside burrows and move very fast, even backwards. Dirt accumulates at the entrance of the burrow, making a mound. The large claws and incisors are used for digging. Obstacles and soil hardness promote changes in direction during burrow construction, yielding a random pattern of burrows. Mound production usually takes place at dusk and at dawn. One single burrow was 111 m long, with 22 mounds above surface; the main burrow constituted 41% of the length with secondary branches constituting the remainder. Mean burrow depth was 50 cm (range 20–118 cm) and diameter was 12.8 cm. This system contained three chambers with food and six empty chambers; three plugged burrows and three nests were also recorded (Sosa, 1981). Burrows immediately below the ground are used mostly for foraging. Lateral burrows frequently are shorter and plugged with fecal pellets and dirt. Deeper burrows are used for nesting activities or storing food (Ceballos and Galindo, 1984; Sosa, 1981).

Activity of *P. tylorhinus* takes place in relatively constant and mild microclimatic conditions. Air temperatures within burrow systems ranged from 25 to 27°C, and relative humidity varied from 44 to 93%. Extreme cases showed that while air temperature inside burrows varied 10.0°C, outside temperatures varied 20.5°C (Sosa, 1981).

Feeding behavior includes carrying and bringing food items as large as complete stems of corn plants into burrows (López-Forment, 1968). However, captive tuzas llaneras store many small pieces of food in a short time and later select diet items. The forefeet handle and shake food before chewing; the food pieces are rubbed against the incisors to eliminate soil particles. After feeding, the individual grooms itself in a similar fashion as *Geomys bursarius* (Vaughan, 1966): front feet are used to clean ears, nape, head, and pockets, and incisors are used to groom venter and chest (Sosa, 1981). The tuza llanera may sleep deeply; body temperature drops little and the animal may be shaken with no immediate response. Its body lies on the ground on one of its flanks with the legs slightly stretched (Sosa, 1981).

Captive males and females are antagonistic. When one tuza llanera is approached by another or by a person, the pocket gopher produces a clicking sound by quickly hitting the upper incisors against the lower incisors. *P. tylorhinus* has never bred in captivity but instead even males and females fight to the death if not maintained in different cages. During combat individuals produce sounds by quickly inhaling and exhaling (Sosa, 1981).

GENETICS. The tuza llanera has a karyotype of 2n = 40 and a FN = 76, based on three males and seven females from 5 mi SW Mazamitla, Colima (Berry and Baker, 1972). All autosomes are biarmed (Fig. 4). The X chromosome is a large submetacentric and the Y chromosome a subtelo-centric. No chromosomal polymorphism has been reported. The 2n and the FN of this species are similar to that for *Pappogeomys fumosus*, *P. zinseri*, and *P. gymnasium*. Analysis of 19 genetic loci for 12 species of geomyids using starch gel electrophoresis revealed *P. tylorhinus* and *P. gymnasium* have a genic similarity (Rogers S) of 0.99, differing only in allele frequency at a single locus. Heterozygosity was zero for *P. tylorhinus* (Honeycutt and Williams, 1982).

REMARKS. Tuza llanera is the accepted vernacular name for this species (Villa-R., 1952). On the basis of morphological and genetic data, members of the subgenus *Crateogeomys*, including *P. tylochinus*, *P. gymnasium*, *P. neglectus*, *P. zinseri*, *P. merriami*,

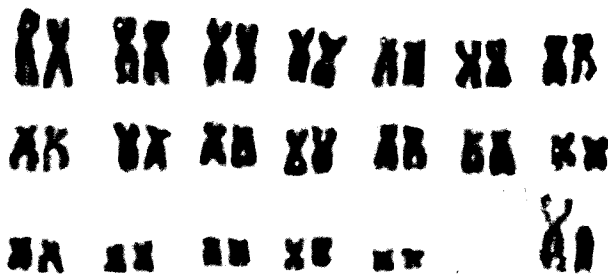


FIG. 4. Karyotype of *Pappogeomys tylorhinus* (after Berry and Baker, 1972).

and *P. castanops*, are included in a genus, *Crateogeomys*, distinct from *Pappogeomys*, that contains *P. bulleri* and *P. alcorni* (Honeycutt and Williams, 1982).

We could not confirm the existence of the locality Mazamitla in the state of Colima, where the specimen referred to by Berry and Baker (1972) was collected. There is a town called Mazamitla in the state of Jalisco approximately 100 km (by road) away from the nearest Colima border. Therefore, the geographical distribution of the tuza llanera shown in Fig. 2 does not include the state of Colima.

The photograph of the karyotype was kindly provided by Robert J. Baker, the distribution map was drawn by M. Carmen Reséndiz, and the skull photos were taken by Demetrio Camarillo. We express our appreciation to "Consejo Nacional de Ciencia y Tecnología, México" (grant P228CCOX891634), the "Dirección General de Asuntos del Personal Académico, Universidad Nacional Autónoma de México" (grant 2009891B), and the MacArthur Foundation (grant 282.311.010) for their financial aid.

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