# Gerbillurus tytonis.
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## Gerbillurus tytonis Bauer and Niethammer, 1959

### Dune Hairy-footed Gerbil

*Gerbillus (Gerbillurus) vallinus tytonis* Bauer and Niethammer, 1959:255. Type locality, "Sossusvlei, Namib Desert, Namibia."

**CONTEXT AND CONTENT.** Order Rodentia, Family Muridae, Subfamily Gerbillinae, Tribe Taterillini, Subtribe Gerbillurina, Genus *Gerbillurus*, Subgenus *Paratatera*. *G. tytonis* was given species rank by Schlitter (1973) and generic status by Davis (1975). No subspecies have been described.

**DIAGNOSIS.** *Gerbillurus tytonis* (Fig. 1) is similar in color and size to *G. paeba* where they coexist, but *G. tytonis* is distinguished by its longer tail (ca. 30% longer than head and body in *G. tytonis*, ca. 20% longer in *G. paeba*), and the different hind feet, with those of *G. tytonis* considerably longer and broader than those of *G. paeba* (length of hind foot = 33.4 mm in *G. tytonis*, 26.5 mm in *G. paeba*). *G. tytonis* has a fringe of hairs on each toe of the hind foot, which is absent in all other *Gerbillurus* species (Griffin, 1990).

Skulls of *G. tytonis* (Fig. 2) are distinguished from those of *G. paeba* by larger tympanic bullae (oblique length ca. 9.8 mm versus <9.0 mm) and shorter posterior palatal foramina (ca. 1.1 mm versus >1.6 mm—Griffin, 1990; Schlitter, 1973). Tympanic bullae of *Gerbillurus tytonis* are smaller than those of *G. vallinus* (oblique length ca 9.8 versus ca. 10 mm—Schlitter, 1973).

**GENERAL CHARACTERS.** *Gerbillurus tytonis* is a small, gracile gerbil with long, broad hind feet. Soles of the feet are well-furred. Upper body is rich reddish or russet brown and underparts are white. The two colors are sharply demarcated; white of the underparts extends to fore and hind feet and well up the flanks. Tail is brown on the dorsum and white on the ventrum, and has a small tassel of gray hairs on the end. Ears are cinnamon buff (Skinner and Smithers, 1990). Fur is loose and long (de Graaff, 1981).

*Gerbillus tytonis* is not sexually dimorphic (Schlitter, 1973). Body mass (mean ± *SE*) for *G. tytonis* collected in the dunes of the Namib Desert is 24.0 ± 0.9 g (*n* = 711—Boyer, 1987). Mean (and range) of external measurements (in mm) for *G. tytonis* are as follows: total length, 225.7 (205–240, *n* = 55); length of tail, 126.5 (113–141, *n* = 55); length of hind foot, 33.4 (28–36, *n* = 57); length of ear from notch, 13 .0 (12–14, *n* = 57—Schlitter, 1973). Cranial measurements (mean and range) in mm for *G. tytonis* are the following: occipitonasal length, 29.3 (28.1–30.4, *n* = 43); breadth across zygomatic arches, 15.6 (14.2–16.6, *n* = 39); greatest breadth of braincase, 13.9 (13.4–14.6, *n* = 43); least interorbital breadth, 5.5 (5.2–6.0, *n* = 57); breadth of rostrum, 4.1 (3.7–4.5, *n* = 56); greatest length of nasals, 11.6 (10.5–13.0, *n* = 55); oblique length of audital portion of auditory bulla, 9.8 (9.3–10.4, *n* = 47); crown length of maxillary toothrow, 4.2 (4.0–4.5, *n* = 50); breadth of palate at M3, 4.9 (4.5–5.3, *n* = 38); length of anterior palatal foramina, 5.4 (5.1–6.3, *n* = 56); length of posterior palatal foramina, 1.1 (0.6–1.6, *n* = 57); greatest height of skull, 12.4 (12.0–12.8, *n* = 29); breadth of auditory bulla, 8.3 (7.9–8.9, *n* = 49—Schlitter, 1973).

**DISTRIBUTION.** *Gerbillurus tytonis* is the only gerbil species permanently resident in the main sand sea of the Namib Desert south of the Kuiseb river from Swakopmund to Luderitz and immediately adjacent areas (Fig. 3; Griffin, 1990). This includes Sossusvlei (Bauer and Niethammer, 1959), Sandwich Harbour, Gobabeb, the Farm Canaan adjoining the diamond area of Namibia

(Meester et al., 1986) and at Far East, Bushman's Circle, and Nara Valley (Boyer, 1987, 1989). It occupies coastal and inland dune systems. No fossils of this species are known.

**FORM AND FUNCTION.** Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16 teeth. At Homeb in the dunes of the Namib Desert, field water turnover rates of *G. tytonis* decreased from 178.0 ml kg$^{-1}$ day$^{-1}$ in November to 98.4 ml kg$^{-1}$ day$^{-1}$ in March (Downs and Perrin, 1990a). Water turnover rate, daily energy expenditure, and assimilation efficiency in the laboratory were 554.1 ml kg$^{-1}$ day$^{-1}$, 2.1 kJ g$^{-1}$ day$^{-1}$, and 91.09%, respectively, when animals were fed a diet of mealworms and carrots without free water, compared to 365.4 ml kg$^{-1}$ day$^{-1}$, 2.56 kJ g$^{-1}$ day$^{-1}$, and 91.95%, respectively, when fed sunflower seeds. When diet was changed from seeds to insects, urine production increased from 0.119 to 0.988 ml/day (Downs and Perrin, 1990b). Maximum urine osmolality varied with diet in the laboratory, from 5.213 osmol/kg on millet seed to 6.129 osmol/kg on mealworms, whereas urine osmolality in the field was considerably less at 3.152 osmol/kg (Downs and Perrin, 1991b). Water turnover rates decrease with decrease in potential water yield of diet in the laboratory (Downs and Perrin, 1990b). Without any succulent material as a supplement, *G. tytonis* maintains body mass on an invertebrate diet but loses mass on a dry seed diet.

Urea concentration varied from 1.813 mM/ml on a diet of mealworms to 4.769 mM/ml on a diet of sunflower seeds; both diets were supplemented with carrots and water. Low resolution mass spectrometric analysis of urine crystalline fractions confirmed the presence of allantoin (Downs and Perrin, 1991a). *G. tytonis* has a simple kidney, with characteristic outer and inner medullary zones and an elongated papilla renis extending into the ureter (Downs and Perrin, 1991a).

Basal metabolic rate of *G. tytonis* is 1.06 ml O$_2$ g$^{-1}$ h$^{-1}$ (72.1% of that expected for its body mass) at thermoneutrality (32.4–34.9°C), and thermal conductance is 0.168 ml O$_2$ g$^{-1}$ h$^{-1}$°C$^{-1}$ (92.3% of that expected by mass—Downs and Perrin, 1990c). Body temperature is regulated from ambient temperatures of 5° to 30°C. *G. tytonis* overcomes high daytime temperatures by nocturnal activity and use of burrows (Downs and Perrin, 1991b).

**ONTOGENY AND REPRODUCTION.** Reproduction and recruitment into the *G. tytonis* population occurs in summer. On the northern fringe of the central Namib Desert dune system at



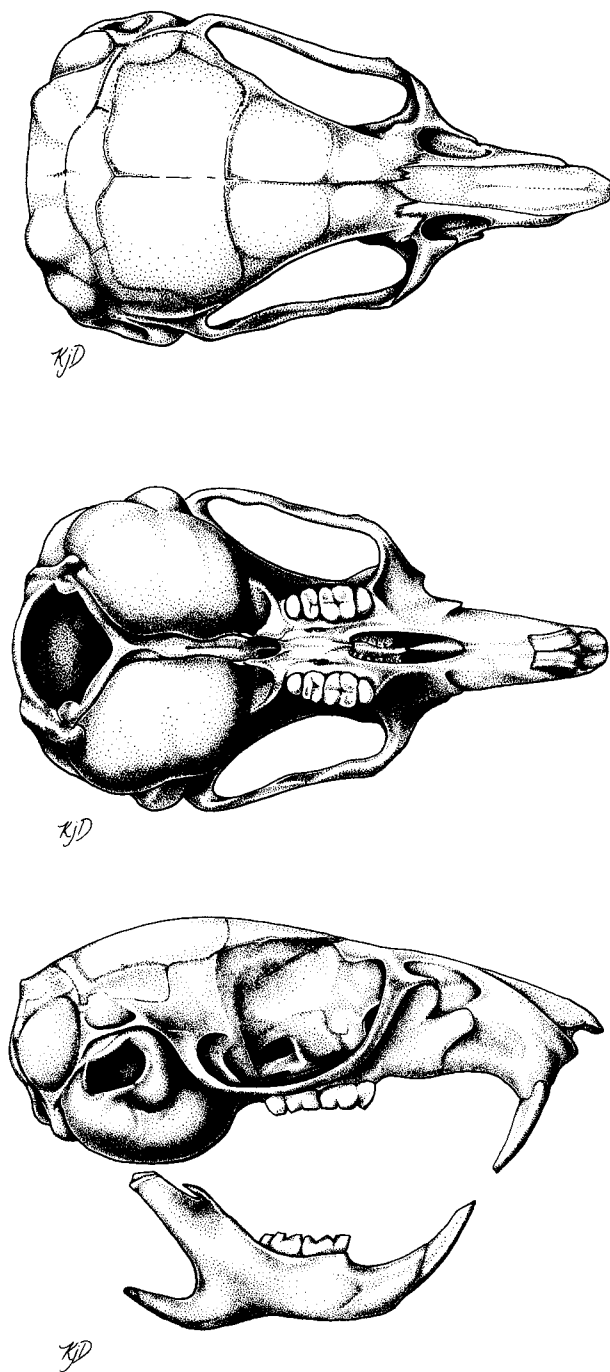FIG. 1. *Gerbillurus tytonis*. Photograph by A. Bruton.

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of mandible of *Gerbillurus tytonis*. Greatest length of cranium is 28.7 mm.



FIG. 3. Distribution of *Gerbillurus tytonis* in southern Africa.

Nara Valley and Bushman's Circle, 48 km and 85 km east of the coast, respectively, *G. tytonis* bred during summer of 1984 and 1985, which is the period of potential rainfall (Boyer, 1987). Adult males had scrotal testes throughout the year. About 25% of females captured between February and May of 1984 were reproductively active, whereas a year later, ca. 50% of females were reproductively active between December and May.

Cyclical changes in vaginal smears ($n = 2$ females, 5 cycles) had a mean duration ($\pm$ *SD*) of 6.2 $\pm$ 1.2 days. A vaginal cast was visible in three unmated females (Dempster and Perrin, 1989*b*). Copulation was observed in two pairs of *G. tytonis* (Dempster, 1990). *G. tytonis* has an unusual pattern of copulatory behavior, with a single ejaculation, lock, and deposition of a copulatory plug. For two observations, the lock lasted 20 and 26 s. Precopulatory
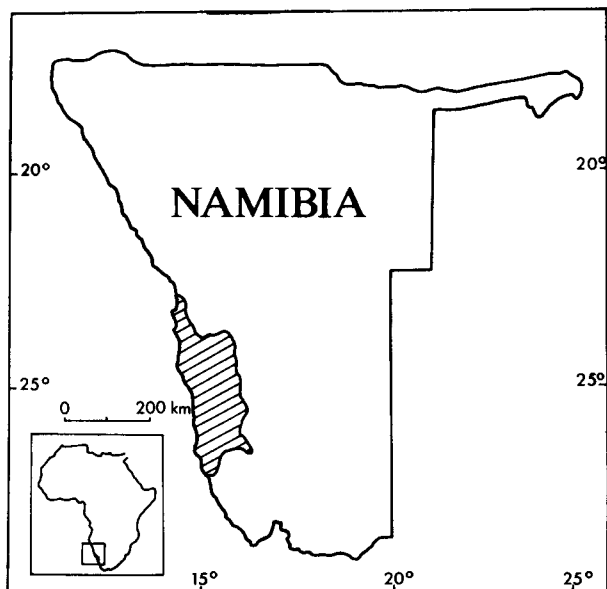
behavior was brief and included several postures which may enhance olfactory communication (Dempster, 1990). Females indicated readiness to mate by stopping adjacent to males, with the forepaws extended anteriorly, but lordosis was not clearly discernible. The male clasped the female while making pelvic thrusts; several deep thrusts indicated that intromission had occurred. Pelvic thrusting ceased once a lock had occurred. After separating, both animals groomed their genitals, both sandbathed, and males marked by perineal dragging. Copulatory plugs were visible in the vaginae of both females after copulation. No further intromissions occurred after ejaculation.

Seven litters of *G. tytonis* have been born and raised in captivity (Dempster and Perrin, 1989*a*). One female *G. tytonis* was observed giving birth to the last neonate of a litter of four pups. Strong abdominal contractions preceded the birth, and the female groomed her anogenital region and rested between contractions. The neonate was expelled while the female was in a quadrupedal posture and the female then consumed the placenta and groomed the neonate. Several bouts of grooming of the young, and of the anogenital region of the female, were interspersed with periods of rest in 2 h following parturition.

At birth, *G. tytonis* has an individual mean body mass of 1.9 g ($n = 22$) and litter size averages 4.4 (range 2–6, $n = 7$—Dempster and Perrin, 1989*a*). Mean length of head and body of newborn individuals is 34.2 mm and mean length of hind foot is 6.5 mm ($n = 17$). At birth, *G. tytonis* weighs 7.6% of adult size and gains 1.6% of adult mass per day during the linear phase of growth (10–50% of adult body size). Neonates are hairless but with vibrissae present on the nose. Ear pinnae are folded flat and fused to the skin of the head in neonates, becoming free at 6–7 days of age. Toes are fused at birth but separate at 6–8 days, whereas hair appears at 10–13 days and eyes open at 22–24 days of age. Walking, jumping, quadrupedal saltation, and sand-digging are evident at 21 days of age. Social interactions, involving mounting between cage mates, aggressive interactions, and allogrooming, occur after 35 days of age.

**ECOLOGY.** *Gerbillurus tytonis* is a terrestrial species that is active at night and seeks shelter in a burrow during daytime. Populations occur in hot, dry areas on shifting red sand dunes of the Namib Desert where the mean annual temperature is >18°C and rainfall is <125 mm/year (Downs and Perrin, 1989). Most *G. tytonis* burrows occur in sand stabilized by vegetation, either *Trianthema hereroensis* or *Stipagrostis sabulicola*. Burrows have one or two entrances, with an average diameter of 55 mm, an average depth of about 285 mm, and an approximate length of 1 m; they may be simple (unbranched) or complex (branched—Downs and Perrin, 1989).

Densities of 17 animals/ha (biomass, 363 g/ha) have been re-

corded (Boyer, 1987), but abundance is highly variable, both spatially and temporally. In May 1984, five of nine *G. tytonis* snap-trapped at Nara Valley were marked animals from a live trap grid 1 km to the north, and four had been live-trapped within the previous 48 h (Boyer, 1987). This suggests extremely large home ranges and foraging distances.

At Far East on the eastern edge of the dune sea (138 km from the coast) that borders on the Pro Namib, *G. paeba* coexists with *G. tytonis*. Habitat preferences facilitate niche segregation because *G. tytonis* prefers zones with high plant species diversity, but avoids compact soils such as interdune valleys, a habitat preferred by *G. paeba* (Boyer, 1987). *G. tytonis* is competitively superior to *G. paeba* in interspecific encounters staged in the laboratory (Dempster and Perrin, 1990*b*) and may exclude *G. paeba* from interdune valleys at certain times (Boyer, 1987). Trapping surveys (Griffin, 1990) in vegetated dunes and the adjacent Kuiseb River bed in 1976 and in the Swakop River bed and adjacent vegetated dunes at Swakopmund in 1978 showed equal abundance of *G. tytonis* and *G. paeba* in dunes, but *G. paeba* was four times more abundant than *G. tytonis* in river bed areas. These years were characterized by high rainfall and high rodent densities.

Predation risk and intra- and interspecific competition influences habitat selection and activity of *G. tytonis* (Hughes et al., 1994). At the Namib Desert Research Unit of Namibia at Gobabeb (23°24'S, 15°03'E), *G. tytonis* co-occurs with the striped mouse (*Rhabdomys pumilio*) in a vegetated island in the dune sea. Both species prefer the same microhabitat (nara; *Acanthosicyos horrida*), although *G. tytonis* also inhabited a second microhabitat (grassland; *Stipagrostis sabulicola*) where predation risk was greater. Two different study techniques (tracking and seed trays) suggest that *G. tytonis* decreased foraging activity in vegetated areas during periods of increased illumination (full-moon periods). Removal of striped mice or conspecifics resulted in a significant increase in the foraging activity of *G. tytonis*. High susceptibility of *G. tytonis* to predation may result in shared occupancy of the safest habitat and competition for limited resources (Hughes, 1990).

Stomach contents of *G. tytonis* from several localities within the Namib Desert suggest an omnivorous diet (Boyer, 1987; Perrin et al., 1992). By volume, seeds, green plant material, and arthropods comprised 7.9%, 36.4%, and 52.6% of the diet respectively at Far East; 17.1%, 45.9%, 33.5% respectively at Bushman's Circle; and 10.4%, 28.9%, and 58.9% respectively at Nara Valley. The amount of green plant tissues in the diet peaked during the hot dry summer (October–January), whereas the maximum intake of seeds occurred during winter (May–October), when 33% of the diet was comprised of seeds. In addition to seasonal variations in diet, marked differences occurred among individuals. Major predators of *G. tytonis* are the spotted eagle owl *(Bubo africanus)* and the black-backed jackal *(Canis mesomelas*—Boyer, 1987).

**BEHAVIOR.** *Gerbillurus tytonis* moves by quadrupedal saltation. Tracks in the desert sand indicate that hind feet are placed anterior to front feet during locomotion across open sand. Distance between successive sets of footprints was ca. 31 cm (*SD* = 10.1—Dempster and Perrin, 1990*c*). *G. tytonis* digs in sand using the forepaws simultaneously to dig sand under the body and then kicks the sand back with the hind feet. Nests are constructed from grass, which is cut into short sections and carried in the mouth. Nests are shaped using the nose and forepaws. Seeds are scatter-hoarded.

The normal sleeping posture is a curled position with the head tucked under the body and the tail curled around the feet. On waking, animals emerge from the nest, stretch, and urinate in a selected spot. Grooming begins with the nose and proceeds in a cephalocaudal sequence. Sandbathing is important in maintaining coat condition in *G. tytonis* (Dempster and Perrin, 1990*c*).

Agonistic behavior of *G. tytonis* has been studied in staged encounters in the laboratory (Dempster and Perrin, 1989*c*, 1989*d*). Four groups of behavior were identified by motivational analysis: these were exploratory and solitary, aggressive, submissive, and sexual. In intraspecific same-sex pairings, *G. tytonis* was the most aggressive and active of all *Gerbillurus* species. Dominance was clearly established in >80% of *G. tytonis* encounters by chasing, attacking, fleeing, and crouching, rather than by fighting.

In intraspecific male-female pairings, female *G. tytonis* dominated males, and behaved aggressively towards unfamiliar males (Dempster and Perrin, 1989*d*). Behavior of *G. tytonis* in staged male-female encounters was characterized by high levels of upright

aggressive postures and low levels of huddling (Dempster et al., 1992).

*G. tytonis* may identify conspecifics by deposited chemosignals. Male *G. tytonis* significantly preferred conspecific odors of females in artificially induced estrus, whereas female *G. tytonis* preferred odors of male *G. tytonis* to those of *G. paeba* (Dempster and Perrin, 1990*a*).

Ultrasonic calling occurs during male-female encounters of *G. tytonis* in the form of a unique stutter vocalization which consists of a series of clicks and a strongly modulated sweep call (Dempster and Perrin, 1991). The sweep calls range from 63 to 48 kHz and have a mean duration of 58 ms (*n* = 61). Stutter calls cover the frequency range 34–11 kHz and have a mean duration of 1,418 ms(*n* = 19—Dempster and Perrin, 1991). Vocalizations are positively associated with sexual and contact-promoting behavior, and rarely accompany non-contact and agonistic behavior (Dempster et al., 1991). Ultrasonic vocalizations accompanied copulation in two observed copulations (Dempster, 1990).

**GENETICS.** *Gerbillurus tytonis* has a diploid chromosome number of 36 with 68 autosomal arms. The standard karyotype of *G. tytonis* is indistinguishable from that of *G. paeba* (Schlitter et al., 1984). Comparison of G- and C-bands of *G. tytonis* and *G. paeba* identified a pericentric inversion in arms 11/12 and the absence of a heterochromatic addition on 33 in *G. tytonis* (Qumsiyeh et al., 1991).

**REMARKS.** *Gerbillurus tytonis* was first described from skulls found in pellets of the barn owl, *Tyto alba* (Bauer and Niethammer, 1959). Its external appearance was subsequently described by Schlitter (1973). The specific name "*tytonis*" is derived from the generic name of barn owls, and means "of tyto".

Morphometric data place *G. tytonis* closer to *G. setzeri* and *G. vallinus* than to *G. paeba* (Schlitter et al., 1984). Pavlinov (1987) performed a cladistic analysis of the genera and subgenera of the Taterillini based on morphological features including structure of the foot, odontological characters, and craniological characters. Cladograms based on morphological characters present a different branching sequence from karyological data (Qumsiyeh, 1986; Qumsiyeh et al., 1991). Based on morphometrics, Pavlinov (1987) proposed that the subgenus *Progerbillurus (G. paeba)* be split first from the subgenera *Gerbillurus (G. vallinus* and *G. setzeri)* and *Paratatera (G. tytonis)*. According to Pavlinov (1987), subgenera *Gerbillurus* and *Paratatera* should be regarded as "species groups" within one subgenus *Gerbillurus. Progerbillurus* should be retained as a subgenus. The cladogram derived from G- and C-banding of chromosomes proposes an unresolved trichotomy, with *G. paeba, G. tytonis* and a separate clade leading to *G. vallinus* and *G. setzeri* diverging at the same time (Qumsiyeh et al., 1991). Skulls were drawn by K. Duxbury.

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