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Cryptomys damarensis.

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Cryptomys damarensis (Ogilby, 1838)

Damaraland Mole-rat

Bathyergus damarensis Ogilby, 1838:5. Type locality "Damaraland, South West Africa."

Georychus lugardi De Winton, 1898:253. Type locality "Kalahari desert, between Palapye and Lake Ngami, north-eastern Bechuanaland."

Georychus micklemi Chubb, 1909:35. Type locality "Kataba river, upper Zambezi, western Northern Rhodesia," Zambia.

Cryptomys ovamboensis Roberts, 1946:315. Type locality "Ondongwa, Ovamboland, South West Africa," Namibia.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricognathi, infraorder Phiomorpha, family Bathyergidae, subfamily Georychinae. *Cryptomys* is polytypic.

DIAGNOSIS. *Cryptomys damarensis* is a medium-sized bathyergid (ca. 131 g) with a range of color morphs from black to fawn; all have a large white head-patch (Fig. 1). The black morph is distinct from other southern African *Cryptomys*. The fawn morph resembles the smaller *Cryptomys darlingi* (ca. 67 g), from which it can be distinguished by body size, mitochondrial DNA sequences (8% divergence), and karyology (*C. damarensis*, 2n = 74–78; *C. darlingi*, 2n = 54).

GENERAL CHARACTERS. Body of *C. damarensis* is cylindrical with a low-slung carriage. Limbs are short and stout, and feet are relatively large with leathery soles. Head is cone-shaped with a blunt, horseshoe-shaped nose. Nares are close together and positioned just above prominent extrabuccal incisors. Eyes are small (microphthalmic) and blue, with thickened eyelids and short eyelashes. Opening to auditory meatus is raised slightly, and external pinnae are absent. Fur is short, thick, and glossy. Color of adult ranges from pale fawn to dark brown–black, even within a colony. Large, white, occipital head-patch of variable shape is present; white middorsal and midventral stripes and white patches may occur. Tactile hairs that project above the pelage occur all over body, particularly on face. Facial whiskers are long (1–2 cm). Short, stiffer hairs border mouth, short tail, and outer edges of hind feet. Oral bristles are deeply stained brown, especially in mature males.

Skull (Fig. 2) is dorsoventrally flattened, with a well-defined sagittal crest. Procumbent incisors are white, ungrooved, and rooted behind last molars in pterygoid region. Zygomatic arch is strongly bowed out. Outer edge of infraorbital foramen is thickened, reducing its size. Angular process of mandible does not extend far backward. Sexual dimorphism is minimal; males tend to be larger, but status within colony affects body size. Nonbreeding males have abdominal testes and a penis within a sheath. Penis of breeding male usually is visible beyond sheath and testes often descend into inguinal pockets. Females have lobed labial flaps and a clitoris that is only exposed during sexual activity. Clitoris and penis are the same length. A vaginal closure membrane is present in nonreproductive females. A breeding female can be identified by a patent vagina and prominent mammae. *C. damarensis* has 6 paired mammae (4 pectoral, 2 inguinal). Body measurements (mean ± *SD*, range, in mm) of 11 wild-caught males and 14 wild-caught females, respectively, are: total length, 189.8 ± 29.2, 109–222, 181.0 ± 15.0, 159–218; length of head and body, 174.3 ± 4.4, 84–196, 159.1 ± 3.9, 139–193; length of tail, 24.0 ± 0.4, 23–26, 22.0 ± 0.5, 21–25; length of hind foot (sine unguis), 31.8 ± 0.4, 29–34, 30.0 ± 0.3, 28–32. Cranial measurements (mean ± *SD*, range, in mm) for 11 wild-caught males and 14 wild-caught females, respectively, are: greatest length of skull, 40.2 ± 0.7, 33.4–41.2, 37.1 ± 0.6, 32.5–39.0; zygomatic width, 30.9 ± 1.1, 23.3–33.0, 26.2 ± 0.6, 23.1–30.0; cranial breadth, 15.8 ± 0.7, 14.7–16.9, 15.3 ± 0.4, 14.5–16.0; length of mandible, 34.7 ± 2.7, 29.9–37.4, 30.6 ± 2.4, 25.0–33.6; height of mandible at coronoid process, 13.8 ± 1.4, 11.2–15.8, 12.7 ± 0.6, 11.9–13.8. Body mass (mean ± *SD*, range, *n*, in g) of wild-caught adult males is 165.0 ± 45.2, 100–281, 281, and that of adult females is 141.5 ± 27.9, 100–230, 290 (N. C. Bennett and J. U. M. Jarvis, in litt.). Nonbreeding males and females are generally smaller than reproductive animals. In captivity, body masses of most individuals range from 80 to 220 g; in exceptional cases, individuals can reach 280 g. Body mass can change with age, food availability, colony composition, and reproductive status (Bennett et al. 1990; Bennett and Navarro 1997).

DISTRIBUTION. *Cryptomys damarensis* is endemic to southern Africa (Fig. 3). It occurs in coarse arenosols in the drier regions of northern South Africa, central and northern Namibia, Botswana, western Zimbabwe, and western Zambia; this is the widest distribution in southern Africa of any species of *Cryptomys*. No fossils are known.

FORM AND FUNCTION. *Cryptomys damarensis* excavates tunnels by using large procumbent incisors. When jaws are fully open during digging, stiff oral bristles push soil particles aside and prevent soil from entering buccal cavity. Two flaps of skin behind extrabuccal incisors prevent entry of soil into esophagus. Forefeet scoop loosened soil backwards and under mole-rat to be collected by hind feet. Once an individual has accumulated a pile, it reverses down the tunnel and uses its small tail, with a fan of stiff hairs, to move soil along like a plough. Soles of hind feet are fringed with stiff hairs along outer edges; these hairs help collect soil during soil transportation.

Damaraland mole-rats are homeothermic and maintain a stable but low body temperature (35.1°C) over an ambient temperature range of 12–33°C (Bennett et al. 1992; Lovegrove 1986). Basal metabolic rate within the thermal neutral zone in terms of oxygen consumption is extremely low for body size (0.66 ± 0.07 $cm^3\ g^{-1}\ h^{-1}$—Bennett et al. 1992; Lovegrove 1986). Thermal conductance in terms of oxygen consumption is high (0.065 $cm^3\ g^{-1}\ h^{-1}\ °C^{-1}$).

Damaraland mole-rats drink no free water and obtain all their fluid requirements from their diet of geophytes (plants with underground storage organs). Geophytes have moisture contents of 77–80% (Bennett and Jarvis 1995) and many bulbs and tubers have a high coefficient of digestibility (85–95%). Hind gut and cecum of *C. damarensis* contain large numbers of cellulose-digesting endo-

FIG. 1. Photograph of Damaraland mole-rats (*Cryptomys damarensis*) from Dordabis, Namibia. Used with permission of the photographer T. P. Jackson.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a nonbreeding adult male *Cryptomys damarensis* from Okavango Swamps, northern Botswana 19°30′S, 23°00′E (Durban Natural Science Museum, DM6708, Durban, South Africa). Greatest length of cranium 39.8 mm. Used with permission of the photographer Andrew Carter.

symbionts including bacteria, fungi, and protozoa. Damaraland mole-rats use digesta from these symbionts through autocoprophagy and absorption of amino acids through the gut wall (Buffenstein 2000).

Cryptomys damarensis obtains essential minerals (such as calcium, magnesium, and phosphate) from geophytes, which are particularly rich in these minerals (Skinner et al. 1991). Damaraland mole-rats have low levels of vitamin D_3 because they are rarely exposed to sunlight, but they can absorb minerals independent of vitamin D_3 very efficiently (Pitcher et al. 1994; Skinner et al. 1991). When minerals are absorbed in excess, blood homeostasis is maintained by storage of excess minerals in teeth and bones (Buffenstein et al. 1995).

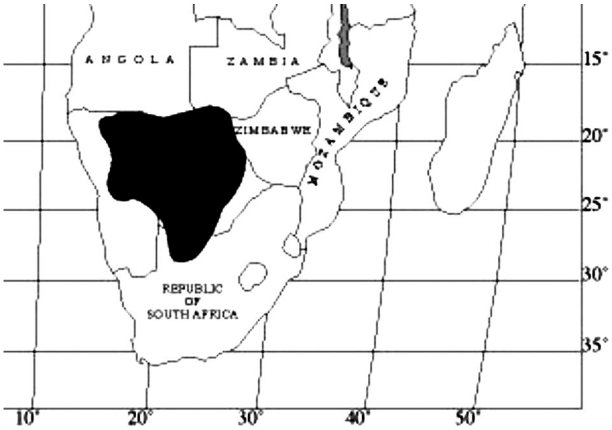

FIG. 3. Geographic distribution of *Cryptomys damarensis* in southern Africa. Map redrawn from Bennett and Faulkes (2000) with modifications.

Premolars and molars are indistinguishable from one another and therefore referred to as molariform. Dental formula is i 1/1, c 0/0, p 0/0, m 4/4, total 20 (De Graaff 1964).

ONTOGENY AND REPRODUCTION. Damaraland mole-rats occur in colonies, which are extended family groups. Reproduction is restricted to a single female in the colony and 1 or 2 males; these breeders are unrelated and usually the founding members of the colony (Bennett and Jarvis 1988; Bennett et al. 1999; Burland et al. 2002; Jarvis and Bennett 1993). Adult nonreproductive members of the colony (offspring of breeders) are reproductively quiescent and physiologically suppressed but not sterile (Bennett 1994; Bennett et al. 1993, 1994). Uteri of nonreproductive females are thin-walled, narrow (<1 mm), and unvascularized. Ovaries are small (<2 mm), smooth, underdeveloped (Bennett 1988), and anovulatory, although developing follicles and luteinized and atretic tertiary follicles are present. Uterine horns of reproductive females are much larger than those of nonbreeding females and have thick walls (2–3 mm). Ovaries of reproductive females are larger than those of nonbreeding females, more lobular in appearance, and show a full range of follicular development (Bennett et al. 1994).

Reproductive tracts of reproductive and nonreproductive males do not differ in gross morphology, but testes of breeding males are heavier relative to body mass. Larger testes in breeders do not result in an increased number of spermatozoa (mean ± *SE*, $0.13 \times 10^6 \pm 0.06 \times 10^6$; $n = 7$ males) relative to nonbreeders ($0.29 \times 10^6 \pm 0.14 \times 10^6$; $n = 21$ males—Faulkes et al. 1994), but sperm viability is impaired in nonbreeders.

Reproductive suppression is mediated through presence of the reproductive female (Bennett et al. 1996). Although her removal results in a recrudescence of ovarian activity in nonreproductive females (Bennett et al. 1996; Rickard and Bennett 1997), mating only occurs if an unrelated male also is present (Rickard and Bennett 1997).

Nonreproductive males have functional gonads, few sperm, and occasionally no sperm (Maswanganye et al. 1999), despite having concentrations of plasma luteinizing hormone and urinary testosterone similar to those of breeding males (Bennett 1994; Bennett et al. 1993). In contrast, nonreproductive females do not ovulate and show reduced follicular development, with tertiary follicles luteinizing or becoming atretic. Lack of ovulation results from inadequate secretion of luteinizing hormone from the pituitary, which in turn is due to an insensitivity of the pituitary to gonadotropin-releasing hormone (Bennett et al. 1993). Mechanisms leading to pituitary insensitivity are not due to inhibition of release of gonadotropin-releasing hormone as a result of endogenous opioid peptides (Molteno and Bennett 2002a). Concentrations of estrogen, luteinizing hormone, and progesterone are lower in nonreproductive females than in the reproductive female (Bennett 1994; Bennett et al. 1993, 1994). Two components to reproductive suppression in females are a suppressive action from the social environment and incest avoidance in the form of obligatory outbreeding. Isolating a nonreproductive female away from the colony releases her suppression and her gonads become active.

Courtship in the Damaraland mole-rat is initiated by the breeding female. On encountering the reproductive male, she vocalizes, briefly drums with her hind feet, and mounts his head. Male and female then chase each other in a head-to-tail fashion in a tight circle. The female pauses, raises her tail, and adopts the lordosis posture. The male smells her genitalia, mounts, and copulates. Mating occurs frequently for ca. 10 days (Bennett and Jarvis 1988).

The reproductive female can produce 3 litters a year. Ovulation is spontaneous (Molteno and Bennett 2000). Gestation length is 78–92 days (Bennett and Jarvis 1988). Mass of the female may increase by 21% during pregnancy. Intervals between litters range from 110 to 167 days, but can exceed 300 days (Bennett et al. 1996). Mean litter size is 3 (range, 1–6). Newborn pups weigh 8–9 g, are mobile, and begin to eat solid food when 6–8 days old. Pelage is present after 6 days, eyes open on day 18, and pups are weaned after 28 days. Sibling sparring begins at 18–25 days, but pups remain within the natal colony.

Rate of growth of pups over the first 80 days is 0.23 g/day (Bennett et al. 1991). In captive colonies derived from a founding pair of Damaraland mole-rats, young in the first 3 litters grow faster and attain a greater body mass than those in subsequent litters (Bennett and Navarro 1997). Body mass at which an individual's growth trajectory reaches an asymptote is variable and depends on size of colony (Bennett et al. 1991; Bennett and Navarro 1997). Assuming a mean adult mass of 100 g and a mean body mass of 9 g at birth, projected time to reach average adult body mass is ca. 430 days in laboratory-reared individuals.

ECOLOGY. *Cryptomys damarensis* occurs in areas characterized by high temperatures (>28°C) and low, unpredictable rainfall (ca. 200–400 mm annually—Bennett and Faulkes 2000). Much of their distribution is closely linked to red Kalahari arenosols, but they also occur in a wide range of coarse sandy soils. Habitat is typically thorn-scrub woodland savanna and grassland with red Kalahari sands and sandy soils. They only occur where geophytes abound.

When excavating tunnels, Damaraland mole-rats push up cores of soil with the same diameter of the burrow; these cores dry and crumble to form the characteristic dome-shaped mound of the molehill. These molehills are the only aboveground evidence of Damaraland mole-rat activity and have 2 distinctive forms. The 1st form is associated with formation of primary exploratory tunnels. The 2nd form is usually associated with feeding and harvesting. Molehills are typically either a single mound, larger than the general mound associated with primary exploratory tunneling, or 2 or 3 mounds in close proximity to each other (Lovegrove and Painting 1987).

Damaraland mole-rats locate food as they excavate superficial (5–25 cm belowground) foraging tunnels. Their diet of geophytes (bulbs, corms, and tubers) includes various members of Cucurbitaceae (e.g., *Acanthosicyos*), Hyanthaceae (e.g., *Dipcadi*, *Ledebouria*, and *Ornithogalum*), and Portulaceae (e.g., *Talinum*). Some of these geophytes are toxic to livestock, but not to Damaraland mole-rats. Storage of selected portable geophytes is based on size; larger geophytes spoil less quickly and are more energetically efficient to transport to the store. Very large tubers (e.g., *Acanthosicyos*) are partially eaten in situ and often regenerated (Jarvis et al. 1998), as are partially eaten bulbs. A colony will occupy the same home range for many years (>6 years) and will only move if its food supplies become exhausted (N. C. Bennett and J. U. M. Jarvis, in litt.).

Tunnels vary in diameter from 65 to 75 cm and burrow length can exceed 1 km. The burrow system is completely sealed from the surface, creating a unique microclimate with moderate temperatures (20°C in winter and 30°C in summer) that are hypoxic (19.9–20.4% O_2) and hypercapnic (0.4–6.0% CO_2) with humidity of >95% (Bennett and Faulkes 2000; Bennett et al. 1988; Roper et al. 2001). Burrow system contains a large network of superficial foraging tunnels (5–25 cm below ground) and a few deeper tunnels (ca. 1.5 m) leading to a nest chamber (ca. 25–30 cm in diameter; located up to 2.5 m belowground) with at least 2 entrances. Nest is lined with bulb, corm, and tuber husks and root epidermis. Close to the nest is a food store with geophytes packed in soil; Damaraland mole-rats sometimes remove buds from stored geophytes that sprout. Blind-ending side tunnels close to nest serve as latrines and are packed with feces and sand. Nature of the substrate limits burrow excavation. Coarse, sandy soils are unworkable for much of the year because the first 40 cm of dry soil is extremely soft and fluid (e.g., sand dunes of the Kalahari). Other soils with high clay or silt content may be impenetrable for much of the year.

Energetic costs of burrowing for food are 500% greater than the resting energetic costs (Lovegrove 1989), and digging costs increase with hardness or extreme softness of soil. Damaraland mole-rats dig most of their foraging burrows when soil is moist; they dig cooperatively to locate sufficient food to sustain the colony when the soil is dry and the energetic costs of burrowing are high (Bennett and Faulkes 2000; Jarvis et al. 1994, 1998; Lovegrove 1991). In arid regions, months may separate good digging opportunities, so full advantage must be taken when it rains. During 2 weeks after significant rainfall, a colony of 16 animals (mass 1.8 kg) extruded 3 metric tons of soil in the form of mounds; this equates to ca. 1 km of tunnels having been excavated by the colony. In this instance, the next opportunity to dig was 1 year later (Jarvis et al. 1998).

Damaraland mole-rats are at risk from predators during formation of molehills. Mole snakes (*Pseudapsis cana*) detect freshly turned soil. A mole snake pushes its head into the soil of a freshly extruded mound, waits for mole-rats moving underground, and then seizes an animal from behind, constricts, and kills it. The cobra (*Naja naja*) also enters open holes and breaks into Damaraland mole-rat burrows. Dispersing Damaraland mole-rats are vulnerable to owls and small carnivores, such as caracal (*Felis caracal*), spotted hyena (*Crocuta crocuta*), black-backed jackal (*Canis mesomelas*), and slender mongoose (*Galerella sanguinea*). Damaraland mole-rats have few parasites. Predominant internal parasites are intestinal nematodes (G. H. Gutjahr, in litt.).

HUSBANDRY. Captive Damaraland mole-rats should be maintained in their social group, preferably in a Perspex (Plexiglas) tunnel system containing a nest area, food chamber, and toilet area. Paper towels or corn husks can be used as nesting material and wood shavings should be placed in the toilet area. Tunnel system should be cleaned weekly and toilet each day. Damaraland mole-rats eat several chopped fruits and vegetables, including apples, carrots, pumpkins, sweet potatoes, and yams. Damaraland mole-rats must be fed daily because they do not drink free water. Temperature of the colony room should be 25–27°C with a relative humidity of 50–60%. Ideally, Damaraland mole-rats are maintained under red light.

BEHAVIOR. Activity in both wild and captive colonies of the Damaraland mole-rat is usually confined to daylight hours, although some activity occurs before dawn and after dusk. Damaraland mole-rats readily entrain to a 12L:12D light cycle (Oosthuizen 2002; Oosthuizen et al. 2003). They exhibit a distinct circadian rhythm of locomotor activity when housed in constant dark, either singly or as a member of a colony (Lovegrove et al. 1993; Oosthuizen 2002; Oosthuizen et al. 2003). The retinohypothalamic tract and associated suprachiasmatic nucleus are fully functional (Oosthuizen 2002).

Damaraland mole-rats are eusocial (Bennett and Jarvis 1988; Jarvis and Bennett 1993). A colony consists of an extended family, which includes the original breeding pair and a number of successive litters; with an overlap of at least 2 generations in the colony (Bennett and Jarvis 1988; Burland et al. 2002; Jarvis and Bennett 1993). Nonreproductive members of the colony cooperatively care for young by defending the colony (sealing damaged entrances of the tunnel system), foraging, and maintaining the burrow system (digging, carrying nesting material, and sweeping). Frequency with which nonreproductive animals perform these activities depends on their body size. As a rule, small (not necessarily younger) Damaraland mole-rats perform digging, foraging, and sweeping tasks much more frequently than do larger (not necessarily older) Damaraland mole-rats. Nonreproductive males and females contribute equally to most tasks, but larger males tend to take on a defensive role and readily threaten and show their incisors if challenged

(Bennett 1990). Alarmed colony members stop moving about the burrow system and violently pump their bodies up and down. Colony members, presumably alerted to danger, are mobilized (Bennett and Faulkes 2000). Colonies tend to be xenophobic and readily accept intruders only after good rains have triggered dispersal (N. C. Bennett and J. U. M. Jarvis, in litt.). Long-term mark–recapture studies reveal little evidence of permanent infiltration from neighboring colonies. Large males occasionally join a colony, but their presence is often transitory (N. C. Bennett and J. U. M. Jarvis, in litt.). Evidence from using DNA microsatellites to determine paternity in colonies supports the inference that transitory males father some offspring (Burland et al. 2004). Colony-specific odors allow individuals to discriminate between colony members and intruders (Clarke et al. 2001; Cooney and Bennett 2000; Jacobs and Reid 1998).

In a functional colony, the oldest nonbreeders are the primary dispersers, but when the breeding female dies the entire colony fragments (Jarvis and Bennett 1993). In both instances, dispersal occurs after rain when costs of digging are lowest, burrows are being extended in search of food, and chances of meeting a mate are highest (Bennett et al. 1996; Jarvis et al. 1994; Molteno and Bennett 2002b). Except in fragmenting colonies, dispersing Damaraland mole-rats of both sexes are adults and are considerably larger than nondispersing Damaraland mole-rats (Hazell et al. 2000). Dispersal takes place both above- and belowground and may occur singly or in cohorts of siblings. Dispersing Damaraland mole-rats must be joined by an unrelated animal of the opposite sex before a new colony can be founded. Cohorts of siblings that disperse together are usually reduced to 1 animal (the new breeder—N. C. Bennett and J. U. M. Jarvis, in litt.). In a long-term field study, 60% of adults disappeared from their natal colony within 16 months of attaining adulthood, and 10% of these were recaptured as founding members of new colonies. These losses were from unsuccessful dispersal or predation (Jarvis and Bennett 1993). In a population of *C. damarensis* in Namibia, 146 animals were <1 year old on 1st capture, and 37% of them remained in their natal colony for at least 16 months, 12.9% for 2–2.5 years, and 8% for >3 years (Jarvis and Bennett 1993).

Nonreproductive females caught before a period of good rains (last rains had been 18 months earlier) exhibited significantly lower pituitary sensitivity to gonadotropin-releasing hormone than did nonreproductive females caught in the same area close to the end of rains. Pituitary sensitivity was not correlated with body mass. Rain appeared to have had a stimulatory effect on the pituitary (Molteno and Bennett 2002b). Damaraland mole-rats caught after the period of good rainfall also were significantly larger than those captured before the rainfall. Rainfall thus provided an opportunity for dispersal with rapid weight gain and enhanced pituitary sensitivity of the reproductive axis. Larger body mass also facilitates dispersal (Molteno and Bennett 2002b).

Colony size is ca. 11 (range, 2–41). Modal size of 110 complete colonies was 12 animals. Reproductive animals are among the largest colony members, and the breeding male is larger than the breeding female. A typical colony has a biomass of ca. 2 kg. Captive colonies have a 1:1 sex ratio at birth (Bennett et al. 1991). A population of all ages in Namibia was skewed toward males (592 males : 461 females—Bennett and Faulkes 2000).

Colonies of the Damaraland mole-rat have distinct dominance hierarchies in which the reproductive male is usually at the apex. Reproductive males and females are the most dominant members of their respective sexes, followed by nonreproductive males and then nonreproductive females. Dominance hierarchy was linear in 3 colonies (Landau's index h = 0.9–1.0—Bennett 1988; Jacobs et al. 1991).

GENETICS. Damaraland mole-rats show low sequence divergence between geographically separated populations. Populations in the Okavango delta (Botswana) and Bulawayo (Zimbabwe), separated by 300 km, have diverged by only 0.55% in cytochrome-*b* genes. Divergence between populations from Botswana and Hotazel (South Africa), separated by 1,000 km, is 1.35%.

Karyotype of *C. damarensis* is 2n = 74–78, with 16 metacentric and 56–60 acrocentric autosomes (Nevo et al. 1986). The X chromosome is metacentric; the Y chromosome is acrocentric. Microsatellite markers indicate that most breeding pairs in wild colonies are unrelated (R = 0.02; close to the population average which by definition is R = 0). Mean colony relatedness (R = 0.46) and mother–offspring relatedness (R = 0.5) are no greater than that for 1st-order relatives (R = 0.52). In Damaraland mole-rat colonies, outbred familial levels of relatedness are sufficient for eusociality (Burland et al. 2002).

CONSERVATION STATUS. *Cryptomys damarensis* is not listed by the International Union for Conservation of Nature and Natural Resources (IUCN) as vulnerable, endangered, or critically endangered (IUCN 2001). This species lives in arid areas with little agriculture and minimal development, so anthropogenic disturbance and eradication are not threats. It is protected in several southern African game parks including Kalahari (South Africa and Botswana), Chobe and Moremi (Botswana), Etosha (Namibia), and Sengwa (Zimbabwe).

REMARKS. Generic name *Cryptomys*, meaning hidden mouse, does not aptly describe the appearance of the mole-rat, which is the size of a small rat. Specific name, *damarensis*, derived from its original capture locality, does not accurately represent its distribution. *C. damarensis* is not restricted to Damaraland and instead occurs over large sections of arid southwestern Africa.

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