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Heterocephalus glaber.

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Heterocephalus Rüppell, 1842

Heterocephalus Rüppell, 1842:99. Type species *H. glaber*.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricognathi, infraorder Phiomorpha, family Bathyergidae. *Heterocephalus* is monotypic (Allen 1939).

Heterocephalus glaber Rüppell, 1842

Naked Mole-rat

Heterocephalus glaber Rüppell, 1842:99. Type locality "die Wiesen-Thäler in Schoa, südlich von Abyssinien," Schoa, Ethiopia.

Heterocephalus phillipsi Thomas, 1885:845. Type locality "Gerlogobie, Ogardain, Central Somali-land."

Heterocephalus ansorgei Thomas, 1903:336. Type locality "Between Ngomeni and Kjinani, Makindu country, British East Africa."

Fornaria phillipsi Thomas, 1903:336. Type locality "Mogadishu, Italian Somaliland."

Heterocephalus dunni Thomas, 1909:109. Type locality "Wardairi, Central Somaliland."

Heterocephalus stygius Allen, 1912:444. Type locality "Neuman's Boma, on the northern Guaso Nyiro River, British East Africa."

CONTEXT AND CONTENT. Context as above. *H. glaber* is monotypic (Honeycutt et al. 1991a).

DIAGNOSIS. Compared with other bathyergid mole-rats (ca. 14 species in 5 genera), the naked mole-rat (Fig. 1) is the smallest and the only one with a long tail, no fur, 3 molars (sometimes 2), and digit 3 of forefoot markedly longer than digit 4.

GENERAL CHARACTERS. Naked mole-rat's body is cylindrical, with back arched dorsally over lumbar and sacral regions (Hamilton 1928). Limbs are short and slender, tapering rapidly toward feet. Head is cone-shaped, blunt anteriorly, with a slightly rounded occipital region. Eyes are tiny with thickened eyelids and minute eyelashes. Prominent jaw musculature occupies much of skull posterior to eyes. Opening to auditory meatus is raised slightly, and external pinnae are absent. Nares are set close together in a horseshoe-shaped region just above base of incisors, and a fold of skin is present above nares.

Naked mole-rat's loose, wrinkled skin is brownish pink in color and darker dorsally than ventrally in young animals; countershading disappears at >7 years of age (Braude et al. 2001). Skin is not concealed by pelage, but isolated tactile hairs occur all over the body, especially on face and tail. Facial whiskers are longest (1–2 cm). Short, stiffer hairs border mouth, eyelids, sides of toes, and outer edges of hind feet.

Body measurements (in mm) of wild-caught adults are (mean ± *SD*, range; *n* = 42—Hagen 1985): total length, 155.8 ± 9.3 (137–180); length of head and body, 116.2 ± 7.13 (103–136); length of tail, 39.3 ± 3.2 (32–47); length of hind foot, 20.5 ± 2.1 (15–31). Skull measurements (mean ± *SD*, range; *n* = 42—Hagen 1985) are: greatest length, 22.9 ± 0.9 (21.0–25.4); zygomatic breadth, 18.3 ± 0.9 (16.9–20.4); cranial breadth, 10.8 ± 0.4 (10.4–12.2); length of mandible, 19.3 ± 1.1 (17.7–22.0); height of mandible at coronoid process, 11.3 ± 0.9 (9.9–13.6).

Mean body mass of wild-caught adults is 33.9 g ± 4.9 *SD* (range, 9–69 g; *n* = 651—Brett 1991a). Nonbreeding males and females do not differ in body mass or length. In captivity, masses of most adults range from 30 to 50 g, but a few individuals may weigh >80 g (Jarvis et al. 1991; Lacey and Sherman 1991). Body mass is variable and can change with age, food availability, colony composition, and social and reproductive status (Jarvis 1985; Jarvis et al. 1991; Lacey and Sherman 1991, 1997; O'Riain and Jarvis 1998; O'Riain et al. 2000).

Skull (Fig. 2) is dorsoventrally flattened, with a long rostrum that tapers anteriorly and houses prominent, strongly pro-odont incisors rooted in the pterygoid bone. Frontals are constricted, and occipital region is well developed. Sagittal and nuchal ridges are present. Zygomatic arches are strongly bowed out, and jugal is supported anteriorly by zygomatic process of maxilla. Infraorbital foramen is small. Angular portion of mandible flares outward, and palate is narrow and sometimes extends behind toothrow (Hill et al. 1957).

Procumbent incisors extend well outside mouth. Incisors are white, lack grooves, and are rooted posterior to last molars. Molars of young have reentrant folds, whereas molars of adults are simple enamel rings; in-folding of lower molars of young persists for longer than in-folding of upper molars. Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Hamilton 1928).

DISTRIBUTION. *Heterocephalus glaber* is endemic to hot, dry regions of eastern Africa (Fig. 3—Honeycutt et al. 1991a). Distribution encompasses most of Somalia, central Ethiopia, and much of northern and eastern Kenya, extending south as far as the eastern border of Tsavo West National Park and the town of Voi.

FOSSIL RECORD. The oldest fossils that resemble *H. glaber* closely enough to be considered ancestral are from Miocene deposits (25–11 MYA) near Karamoja, Uganda (Brett 1986). The 2nd oldest, similar-looking fossil is from the Kakesio Beds (4.3 MYA), south of Laetoli, Tanzania (Denys 1989). Neither of these fossils has been named. Three named ancestral species are *H. quenstedti*, from Pliocene deposits (3.7–3.5 MYA) at Laetoli (Dietrich 1942); *H. atikoi*, from Pleistocene deposits (2.5–1.8 MYA) at Omo, Ethiopia (Wesselman 1982); and *H. jaegeri*, from Pleistocene deposits (1.7 MYA) at Olduvai, Tanzania (Denys 1989). *H. jaegeri* fossils occurred in Olduvai beds until ca. 0.8 MYA but then disappeared (Denys 1989).

FORM AND FUNCTION. Naked mole-rats live in hypoxic, hypercapnic, subterranean burrows (Bennett and Faulkes 2000; Buffenstein 1996, 2000; Jarvis and Bennett 1991; Stein 2000). Blood has a high oxygen affinity (P_{50} = 23.3—Johansen et al. 1976), lungs are minimally developed (Maina et al. 1992),

FIG. 1. Naked mole-rats (*Heterocephalus glaber*), a pregnant female (center) and nonbreeders in the nest chamber. The female bore 27 pups the next day. Photograph by J. U. M. Jarvis.

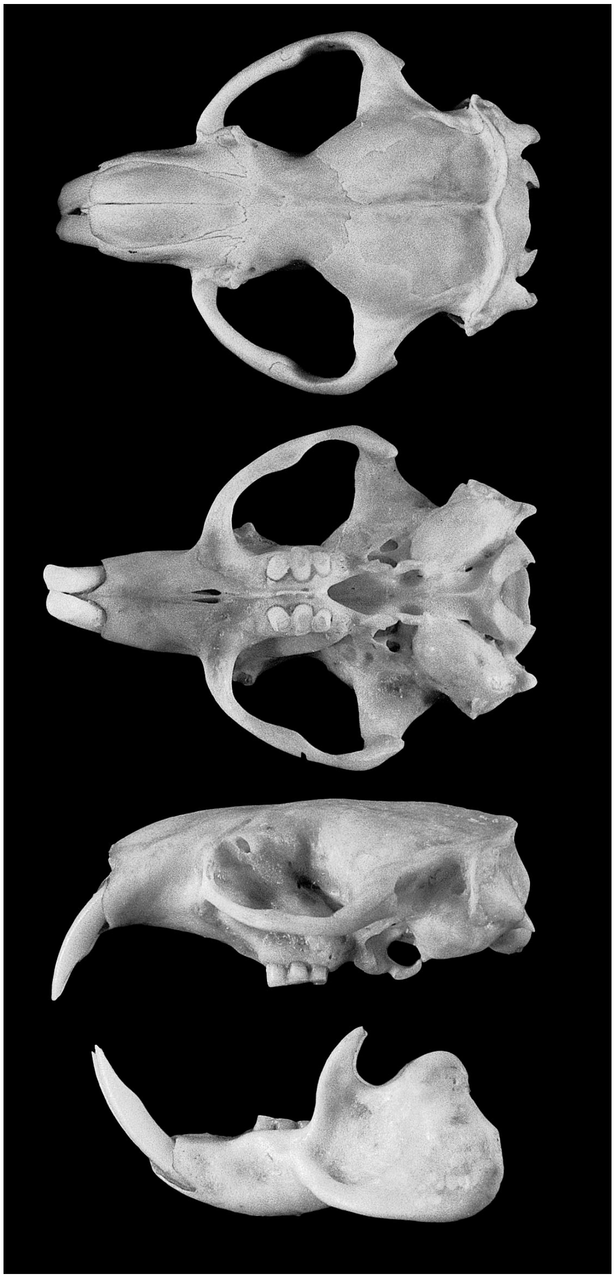

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Heterocephalus glaber* from Lerata, northern Kenya (nonbreeding female, University of Cape Town, South Africa; photographs by N. Eden). Greatest length of cranium is 27 mm.

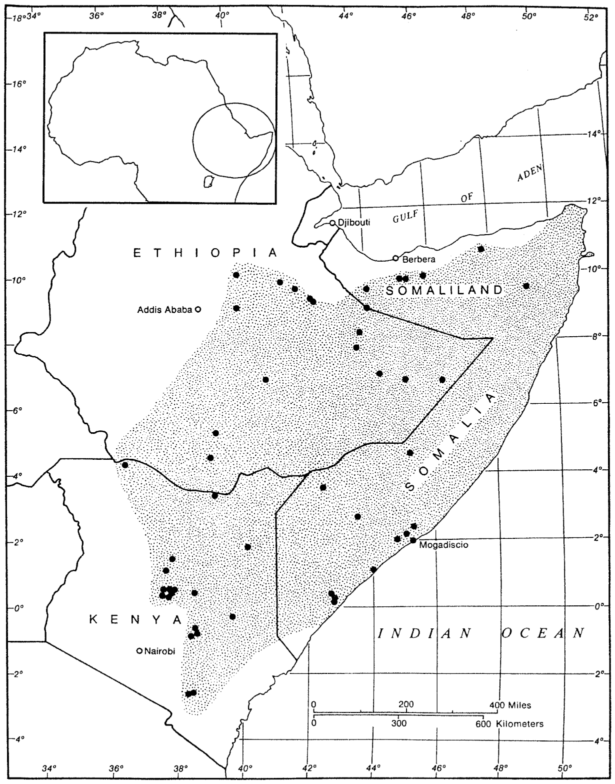

FIG. 3. Distribution of *Heterocephalus glaber* in eastern Africa (modified from Honeycutt et al. 1991a).

and basal metabolic rate is extremely low for body size (ca. 0.70 ml O_2/g-h—McNab 1966, 1979). Metabolic rate decreased by 25% when food was restricted for 16 days (Goldman et al. 1999). In nature, foraging is severely restricted during dry seasons (Brett 1991b).

Naked mole-rats are essentially poikilothermic across ambient temperatures of 12–37°C (Buffenstein and Yahav 1991a). They regulate body temperature primarily through heat exchange by conduction. To warm up they bask against walls of shallow burrows heated by the sun, and to lose heat they move to deeper, cooler burrows (Brett 1986, 1991b). Maximum conduction occurs by pressing against the substrate and increasing peripheral circulation to the thin skin (Buffenstein and Yahav 1991a). Heat exchange is enhanced by skin folding, a minimal fat layer, and considerable vascularization. Naked mole-rats also huddle together in the nest (Withers and Jarvis 1980; Yahav and Buffenstein 1991). Breeding females maintain a higher body temperature when pregnant by increasing metabolic heat production and frequency and duration of basking (Buffenstein et al. 1996; Urison and Buffenstein 1995).

Naked mole-rat's loose skin allows the body to move around within the integument, enhancing flexibility and protecting internal organs when squeezing through narrow spots in tunnels. Epidermis is 1–14 cell layers, depending on body location (Tucker 1981), is well vascularized, and has few sweat glands (Thigpen 1940; Tucker 1981). Some adipose tissue occurs in the dermis in association with sparse hair follicles. Pigment cells occur in the dermis (Daly and Buffenstein 1998). Sensory hairs are present over much of the body, with greatest concentrations on muzzle and tail (Hamilton 1928).

Incisors grow continuously but are worn down during tunnel excavation. Incisors are sharpened by filing lower and upper teeth against each other (Jarvis 1969; Lacey et al. 1991). Jaw muscles constitute ca. 25% of the animal's total muscle mass in *H. glaber* (T. Grand, vide Sherman et al. 1992). When jaws are fully opened during digging, buccal evaginations close off oral cavity (Tucker 1981).

Pineal gland is 0.0021 mm^3 (Quay 1981). Areas of neocortex devoted to vision in other rodents are greatly reduced (Catania and Remple 2002), whereas areas associated with touch and control of oral cavity and teeth are hypertrophied, e.g., 31% of the primary somatosensory cortex is devoted to representation of incisors (Catania and Remple 2002). Naked mole-rat's eyes are small, and visual acuity is poor (Hefner and Hefner 1993). Although anatomical and biochemical components of the visual system are present, corneal electroretinogram recordings revealed no physiological responsiveness (Hetling et al. 2000). However, naked mole-rats show a startle response when strongly illuminated.

Naked mole-rats do not drink water. They obtain moisture from succulent foods (tubers, bulbs, and geophytes), even though some of these foods may be high in salts. Maximum urine-concentrating ability of naked mole-rats is ca. 1,500 mmol/kg (Urison and Buffenstein 1994).

Naked mole-rats eat low-quality, high-fiber diets. Digestive efficiencies are >88% (Buffenstein and Yahav 1991b), which is largely due to symbiotic microorganisms in the enlarged hind gut, especially the caecum (Hill et al. 1957; Porter 1957). Endosymbionts ferment indigestible cellulose and fibers into short-chain, volatile fatty acids, which provide a substantial fraction of basal energetic requirements (Buffenstein 2000). Caecal temperatures are at least 1°C lower than temperatures measured simultaneously within the peritoneal cavity or rectum (Yahav and Buffenstein 1992). Naked mole-rats regularly reingest partially digested fecal pellets (Jarvis 1991a; Lacey et al. 1991). Autocoprophagy contributes to digestive efficiency, reinoculates the individual with endosymbionts, and provides an additional source of protein and energy from digestion of the microbes themselves (Dyer 1998).

Naked mole-rats obtain essential minerals such as calcium, magnesium, and phosphate from their vegetable diet as well as from partially buried bones of large ungulates (Brett 1991b). Although they have low levels of vitamin D3 (they are rarely exposed to sunlight), naked mole-rats absorb the minerals via specialized vitamin D_3–independent paracellular processes (Buffenstein et al. 1993, 1994). When minerals are absorbed in excess, blood homeostasis is maintained by storage in teeth and bones (Buffenstein et al. 1995; Yahav et al. 1993).

Uteri of nonbreeding females are thin-walled and narrow (ca. 1 mm wide), and ovaries are small, thin, flat structures (ca. 2 mm long) that contain mainly primordial and primary follicles (Kayanja and Jarvis 1971). Lack of ovarian development is due to inadequate secretion of luteinizing hormone (LH) from the pituitary as a result of its insensitivity to gonadotropin-releasing hormone (GnRH—Faulkes et al. 1990b), which itself is due to minimal hypothalamic secretion of GnRH (Faulkes and Abbott 1997). Uterine horns of breeding females are wider and thicker-walled (exact dimensions vary with the reproductive cycle). Ovaries of breeding females are 2–3 times larger and thicker than ovaries of nonbreeding females.

External genitalia show minimal sexual dimorphism. Males have abdominal testes, and most females have a vaginal closure membrane. Penis and clitoris are about equal in length. Perineal muscles and motorneurons are sexually monomorphic (Peroulakis et al. 2002). Genitalia of nonbreeding females are distinguished from those of males by a darkish horizontal line, which marks the position of the closed vagina, between clitoris and anus. Breeding males are generally large, emaciated in appearance, and have a more prominent raised area around penis than do nonbreeding males (Jarvis et al. 1991; Lacey and Sherman 1991). Breeding females can be identified easily by large size, weight, elongate shape (Jarvis 1991a; O'Riain et al. 2000), swollen and raised genital area, patent vagina, and presence of well-developed mammae (Sherman et al. 1999).

Mean number of mammae is 11.9 ± 1.2 *SD* (range, 9–15—Sherman et al. 1999). Means and ranges are identical for males (n = 206) and females (n = 249) and for breeders and nonbreeders. Many individuals (61%) have different numbers of mammae on left and right sides of the body. Numbers of mammae and fluctuating asymmetries in mammary numbers do not depend on an individual's sex or breeding status, or whether it was wild-caught or born in captivity (Sherman et al. 1999). Just before parturition, nipples of nonbreeding males and females often enlarge, although only the breeding female lactates (Jarvis 1991a).

Males may lose up to 30% of their body mass once they become breeders (Jarvis et al. 1991). Reproductive tracts of breeding and nonbreeding males do not differ in gross anatomy, but breeding males have prominent sperm-storage sacks just distal to vas deferens, whereas those of nonbreeding males are undeveloped (Faulkes et al. 1994). Among wild-caught males, 76% (n = 84) had spermatozoa in their vasa differentia (Jarvis 1991a). However, mean numbers (±*SD*) of spermatozoa are higher in breeding than in nonbreeding males ($8.59 \pm 2.69 \times 10^6$ versus $1.78 \pm 1.43 \times 10^6$). Proportions of spermatozoa that are motile and normal in shape also are higher in breeders than in nonbreeders (Faulkes et al. 1994).

Nonbreeding males have a lower LH response to a single, 0.1-μg injection of exogenous GnRH than do breeders (nonbreeders: range, 1.5–8.9 mi.u./ml, n = 5; breeders: range, 10.0–45.1 mi.u./ml, n = 4—Faulkes and Abbott 1991; Faulkes et al. 1991a).

ONTOGENY AND REPRODUCTION. Naked mole-rats live in colonies, which are extended family groups. Within colonies, reproduction is restricted to 1 female (occasionally 2) and 1–2 males (occasionally 3—Jarvis 1991a; Lacey and Sherman 1991; Sherman et al. 1992). Nonbreeders are not physiologically sterile, but they are sociologically suppressed by aggressive dominance of the breeding female. Reproductive suppression is not mediated by the breeding female's primer pheromones (Faulkes and Abbott 1993, 1997).

Individuals become sexually mature when breeding opportunities arise. First conception in females is from 7.5 months of age to ≥16 years. First mating in males is from 9.0 months to ≥17 years (Sherman and Jarvis 2002). A 21.7-year-old female bore a litter of 21 pups and raised 2 of them a month before she died.

A breeding female's reproductive cycle lasts ca. 34 days (follicular phase, 6 days; luteal phase, 28 days—Faulkes et al. 1990a). Breeding occurs year round, and females can bear litters every 76–84 days (Brett 1991a; Jarvis 1991a; Lacey and Sherman 1991). Gestation is 66–74 days (Jarvis 1991a). Estrus occurs ca. 10 days postpartum, and the breeding female solicits copulations from 1–3 males. Polyandrous mating can result in multiple paternity within a litter (Faulkes et al. 1997a). Lactation lasts 5 weeks.

During a breeding female's 1st few pregnancies, her lumbar vertebrae elongate, resulting in irreversible changes in length and size of her body cavity (Jarvis et al. 1991; O'Riain et al. 2000). Breeding females with fully elongated bodies have significantly larger litters than do those that have recently attained breeding status. The breeder's elongated body is associated with hypertrophy of the alimentary canal.

Body mass of an established breeding female may increase by up to 84% during pregnancy, and she often has difficulty in moving through narrower tunnels (Jarvis 1991a). The breeding female's energy demands increase by ca. 1,300 kJ per gestation cycle; lactation requires an additional 1,515 kJ per day for an average-sized litter (Urison and Buffenstein 1995).

Field-caught litters average 11.3 pups ± 6.2 *SD* (range, 1–28; n = 82), and captive-born litters average 11.4 ± 5.6 pups (range, 1–27; n = 190—Sherman et al. 1999). Wild and captive breeding females routinely bear >50 pups/year in 4–5 litters (Braude 2000; Jarvis 1991a). One wild-caught female bore >900 pups during 11 years in captivity (Sherman and Jarvis 2002). Litter sex ratio at birth is 1:1 (Jarvis 1991a). Sex ratio is male biased (1.4:1) among adults in captive and wild colonies (Braude 1991a; Brett 1991a; Jarvis 1985; Sherman et al. 1992).

Newborn pups are bright pink in color and weigh 1–2 g (Jarvis 1991a). Abdominal viscera, cranial sutures, and much of the skeleton are visible through their thin, translucent skin. Eyes and auditory meatus are sealed, digits are fused but discernible, and scattered sensory hairs are present. Within 24 h of birth, incisors erupt, and pups begin to crawl unsteadily. Multiple young nurse, sequentially, from the same nipple (Sherman et al. 1999). Auditory meatus opens on ca. day 14, and pups begin reacting to noise. As movements become increasingly coordinated, young begin leaving the nest (O'Riain 1996). At ca. 3 weeks they start play fighting by locking incisors and pulling and pushing each other or dragging each other by the skin or tail. Weaning gradually occurs over several weeks: pups first beg for caecotrophes from nonbreeders and nibble on plant materials when they are ca. 2 weeks old, first practice autocoprophagy when ca. 4–5 weeks old, and are weaned when ca. 5 weeks old. At around weaning, pups begin to perform colony-maintenance behaviors such as sweeping soil and carrying food (Lacey and Sherman 1991).

Growth of *H. glaber* pups during the first 11 weeks is 0.16–0.21 g/day (Bennett and Faulkes 2000; Bennett et al. 1991; O'Riain 1996). In captive colonies begun from a pair of animals, young in the 1st litters eventually attain greater body mass than do those in later litters (Jarvis et al. 1991; O'Riain and Jarvis 1998). Body mass at which each individual's growth curve reaches a plateau is variable and depends on colony size, and social and reproductive status (Jarvis et al. 1991; Lacey and Sherman 1997; O'Riain and Jarvis 1998). Pups that die are consumed (Jarvis 1991a).

ECOLOGY. Naked mole-rats live in arid habitats, characterized by high temperatures and low and irregular rainfall, which generally averages 200–400 mm/year (Brett 1991a). They are found most frequently in hard, consolidated, lateritic loams, although they can live in fine sand, pure gypsum, and laterite (Brett 1991b; Hill et al. 1957; Jarvis 1985).

Colonies contain from ≤10 to ≥290 individuals, with an average of 75–80 animals per colony (Braude 1991a, 2000; Brett 1991a). Colony sizes are positively correlated with the coefficient of variation in rainfall and inversely correlated with mean distances between food sources and numbers of months in which rainfall exceeds 25 cm (Faulkes et al. 1997b; Jarvis and Bennett 1993; Jarvis et al. 1994; Lovegrove and Wissel 1988).

Naked mole-rats feed on a variety of bulbs, roots, and tubers, including *Anthericum venulosum*, *Chloris roxbergiana*, *Coccinia microphylla*, *Cyperus niveus*, *Dactyliandra stefaninii*, *Macrotyloma maranguense*, *Pyrenacantha kaurabassana*, *Stylochiton salaamicus*, *Talinum caffrum*, *Thunbergia guerkeana*, *Vigna friesiorum*, and *V. membranaceae* (Brett 1991b). Foraging burrows are finely branched when the animals encounter patches of small vegetative tubers (e.g., *M. maranguense*) but not when they encounter large, isolated geophytes (e.g., *P. kaurabassana*—Brett 1991b). Naked mole-rats partially consume large tubers, fill them with soil, and return to feed on them later (Brett 1991b).

Energetic costs of tunneling for food are ca. 300–500% greater than resting levels (Lovegrove 1989), and digging costs increase with hardness of the soil. Naked mole-rats cannot search extensively for new food sources unless the ground has been sufficiently moistened by rainfall (Jarvis et al. 1994). During brief periods after rain, colony members must cooperate and dig intensively to find enough food to sustain them through the long, irregular droughts (Jarvis 1978; Lovegrove 1991).

A colony's burrow length is variable, depending on colony size and local food abundance (Brett 1991b). One completely excavated burrow system of a colony of 60 animals was 595 m long (Jarvis 1985). Another colony (85–90 animals) had a network of burrows that was ca. 3 km long and included 11 nest chambers. Although burrows of neighboring colonies are often 100s of meters apart, where food is abundant colonies may lie within 10s of meters (Braude 2000; Brett 1991b).

On the surface above burrows are clusters of volcano-shaped mounds. Immediately below is a network of narrow (2.5–3-cm diameter) superficial tunnels (2–20 cm deep), which are just wide enough for animals to move through in single file and which lead to patches of bulbs. Superficial tunnels are blocked off after naked mole-rats have finished foraging in an area. Leading downward from superficial tunnels are slanting connecting burrows, 0.5–1.0 m long. These are typically higher than they are wide, and individuals can pass over each other. Connecting burrows end in wide (4–5-cm diameter), relatively unbranched burrows. These are the colony's main tunnels. If they are experimentally bisected, they are soon rejoined. Nest chambers are accessed from wide tunnels via several entrances and usually contain tuber husks, root skins, and other food remnants. Associated with nest chambers are bolt-holes that descend steeply for several meters and end abruptly. Several blind-ended outpocketings off the wide tunnels contain urine and hard-packed feces (Brett 1991b; Hill et al. 1957; Jarvis 1985; Jarvis and Sale 1971). Burrows ≥30 cm below ground are warm (26–32°C—Brett 1991b) and humid (ca. 80%—McNab 1966) year round.

New colonies can form by fissioning when a small group splits off and plugs connecting tunnels with earth. In the absence of aggression from the breeding female, reproductive suppression is released, allowing new breeders to mature sexually. This process was observed in a captive colony (Lacey and Sherman 1997) and inferred in neighboring field colonies based on proximity (Brett 1991a) and close genetic relationship (Faulkes et al. 1990c, 1997a; Honeycutt et al. 1991b; Reeve et al. 1990).

Dispersers can also found colonies. Disperser morphs are very active, have large fat stores, seek copulations with members of foreign colonies rather than attack them (O'Riain et al. 1996), and preferentially outbreed (Ciszek 2000; Clarke and Faulkes 1999). In captivity, 1–2 especially fat and active individuals were produced in 6 of 48 (13%) colonies containing over 40 mole-rats (O'Riain et al. 1996). In the field, individuals with similar morphologies were produced by 6 large colonies among 24 colonies (O'Riain and Braude 2001). Dispersers sometimes travel >200 m above ground (Heaton 1998; Braude 2000). However, of 21 nascent colonies containing 1–4 emigrants from nearby colonies (Braude 2000), only 1 colony survived >1 year (O'Riain and Braude 2001).

Naked mole-rats are preyed on by snakes, especially rufous-beaked snakes (*Rhamphiophis oxyrhynchus*); sand boas (*Eryx colubrinus*); and various raptors (Braude 1991b, 2000; Brett 1991a; Hill et al. 1957).

In Meru National Park, Kenya nonbreeding males and females were recaptured in their natal colony for 1–3 years on average and >10 years at the maximum (Braude 2000; Braude and Ciszek 1998). Wild colonies lost 12–91% of their workers per year ($\bar{X}$ = 46% ± 23 *SD*—O'Riain and Braude 2001), whereas the probability that a breeding female would disappear between years was only 0.07 (Braude 1991a). In captivity, naked mole-rats commonly live >15 years (*n* = 86 individuals in 25 colonies), and longevities of females and males, or breeders and nonbreeders, do not differ (Sherman and Jarvis 2002). Maximum longevity of a breeding male in captivity is 28 years and 2 months (Buffenstein and Jarvis, in litt.) and of a breeding female, 23 years and 8 months (Sherman and Jarvis 2002).

Lack of fur reduces ectoparasites (Lacey et al. 1991). Freshly captured animals may harbor cutaneous (*Androlaelaps*—Lacey et al. 1991) and subcutaneous (*Muridectes heterocephali*—Braude 1991a; *Actotylopus canestrinii*—Fain 1968; Parona 1895) mites and chiggers (*Euschongastia botegi*—Parona 1895).

BEHAVIOR. Captive *H. glaber* colonies are active round the clock and do not exhibit circadian activity cycles or entrain to light cycles (Davis-Walton and Sherman 1994). However, 10 of 15 isolated individuals exhibited circadian patterns of wheel-running activity; these 10 animals could be entrained to light and temperature cycles (Riccio and Goldman 2000).

Touch-sensitive hairs inform the animal of its surroundings and help it navigate in darkness (Crish et al. 2000). When individuals run forward, they move their head from side to side, keeping whiskers in contact with tunnel walls; when they run backward, they move their tail from side to side, again maintaining tunnel contact (Lacey et al. 1991).

Naked mole-rats are eusocial (Jarvis 1981; Sherman et al. 1991, 1992, 1995). Colonies are extended family groups, with overlapping generations (Braude 1991a; Brett 1991a). Reproduction is extremely restricted (Jarvis 1991a; Lacey and Sherman 1991), and nonbreeders cooperate to care for and defend the reproductives and young (Lacey and Sherman 1991, 1997).

Breeding females can bear and raise large litters because they are fed and protected by nonbreeding colony members (Sherman et al. 1999). Nonbreeding males and females (usually the siblings) contribute equally to care of newborns and to maintenance and defense of the burrow system (Faulkes et al. 1991b; Jarvis 1991a; Lacey and Sherman 1991, 1997). Nonbreeders huddle with pups, handle and groom them, retrieve them if they wander out of the nest, and evacuate them during disturbances. Nonbreeders also dig new tunnels, harvest and bring back food, clear tunnels of protruding roots, construct nests, plug tunnel breaks, and attack predatory snakes and invaders from foreign colonies. Finally, nonbreeders provide caecotrophes for the breeding female and the 2–3-week-old pups (Lacey et al. 1991).

Nonbreeders vary in frequencies of performing particular tasks, depending on body size and age (Jarvis 1991a; Jarvis et al. 1991; Lacey and Sherman 1991, 1997; O'Riain and Jarvis 1998). Small (usually younger) animals are the primary maintenance workers and also the most active in pup care. Large nonbreeders, with massive incisors, are the main colony defenders (Lacey and Sherman 1991) and the most active volcanoers (Braude 1991b). Individuals gradually switch from maintenance to defense activities as they age. However, age polyethism is frequently obscured by behavioral and size changes associated with variations in colony composition and competition to fill reproductive vacancies (Lacey and Sherman 1991, 1997).

Although the largest individuals in a naked mole-rat colony are usually the oldest (Lacey and Sherman 1991, 1997), early social influences can affect growth rates and precise roles in the colony's work force. Individuals born to mature colonies remain small maintenance workers for many years, whereas individuals born in incipient colonies grow larger and become defenders, dispersers, or breeders (O'Riain and Jarvis 1998).

Naked mole-rats dig with procumbent incisors, not forefeet. When jaws are fully opened during digging, stiff oral bristles push dirt particles aside. Captive individuals sometimes lodge a wood chip or tuber husk behind their incisors and in front of their lips and molars while digging in fine soils (Shuster and Sherman 1998). This helps prevent choking or aspiration of fine particulate debris.

Naked mole-rats form digging chains, in which the 1st individual gnaws at the blind end of a tunnel and a series of colony members sweep loosened dirt back along the burrow to a large individual who kicks it onto the surface (Braude 1991b; Jarvis and Sale 1971). This creates a volcano-shaped mound with a central hole and is the only above-ground evidence of a naked mole-rat colony. In 1 year a colony of 85–90 mole-rats produced 400–500 molehills, the equivalent of 3,600–4,500 kg of soil and 2.3–2.9 km of new burrow (Brett 1991b). This colony moved up to 13.5 kg of soil to the surface per hour. The animals work quickly because until the volcano hole is sealed off, it offers access to snakes and driver ants (Braude et al. 1999; Brett 1991a). The volcanoer is particularly vulnerable to predators (Braude 1991b). Most molehills (70%, $n = 120$) are produced between 0200 and 0800 h, when predatory snakes are least active (Brett 1991b).

Colonies are xenophobic and defend their burrow system (and its food supplies) by attacking intruders (Lacey and Sherman 1991; O'Riain and Jarvis 1997). Long-term mark-recapture studies of field colonies reveal no evidence that neighboring colonies mix (Braude 2000; Brett 1991a). Colony-specific odors enable individuals to discriminate colony mates from strangers. A colony's unique odor is refreshed by rolling and scratching in communal toilet and nesting areas. Naked mole-rats lose the distinctive colony odor when removed for a few days (O'Riain and Jarvis 1997). Chemical cues are involved in kin recognition by the breeding female (Reeve and Sherman 1991) and recognition of the breeding female by her pups before their eyes open (Jarvis 1991a).

When an individual finds a new food source, it returns to the nest, laying down an odor trail and giving a special vocalization that alerts colony mates. Recruits follow the odor trails of successful scouts to locate food sources (Judd and Sherman 1996).

The vocal repertoire of *H. glaber* contains at least 18 distinct categories of vocalizations (Pepper et al. 1991) over a narrow auditory range (65 Hz–12.8 kHz at 60 dB—Hefner and Hefner 1993). Most vocalizations are 1–9 kHz in frequency with durations <200 ms (Judd and Sherman 1996; Pepper et al. 1991). Naked mole-rats are most sensitive to low-frequency sounds, which attenuate less in soil than those with high frequencies (Francescoli 2000), and can localize sounds emanating from in front of or behind their body more accurately than sounds produced laterally (Hefner and Hefner 1993).

Vocalizations include food recruitment calls, high-pitched contact and aggressive chirps, a mating call, toilet-assembly call, and vocalizations specific to pups, such as squawks when pups are stepped on and caecotroph-solicitation chirps. Many calls are associated with alarm (Pepper et al. 1991). If a small maintenance worker encounters a foreign object in a tunnel, it usually "taps" or "sneezes," which recruits other small workers from nearby. However, if the worker encounters a snake or a member of a foreign colony, it rushes off toward the nest "screaming." This mobilizes large-bodied defenders, who begin chirping and running to the site (Lacey and Sherman 1991). There, they threaten the intruder with open mouths and snapping teeth and make either grunting sounds (predators) or hisses and aggressive trills (foreign colonies).

Within colonies the breeding female is the most active and aggressive individual (Clarke and Faulkes 2001; Lacey and Sherman 1991; Reeve and Sherman 1991). When the breeding female encounters colony members in tunnels, she either shoves them backward or walks over them, rather than passing side by side (Clarke and Faulkes 1997; Jarvis 1991a). Aggression by the breeding female reduces the reproductive development of subordinates (Clarke and Faulkes 2001; Faulkes and Bennett 2001; Jacobs and Jarvis 1996). Aggression by breeding females is primarily directed toward larger, older nonbreeders of both sexes (Jacobs and Jarvis 1996; Reeve and Sherman 1991). Sometimes (O'Riain 1996; van der Westhuizen 1997), but not always (Reeve and Sherman 1991), these are her closest kin. Large nonbreeders are least likely to spontaneously engage in colony maintenance activities when the breeding female is absent and most likely to attempt to supersede her when she is present (O'Riain 1996; Reeve and Sherman 1991; van der Westhuizen 1997). In some colonies, nonbreeders respond to being shoved by increasing their work levels, and temporary removal of the breeding female results in decreased colony maintenance activities (Reeve 1992; Reeve and Sherman 1991). In other colonies the breeding female preferentially shoves already active animals, and temporary removal of the breeding female does not result in decreased activity levels (Jacobs and Jarvis 1996).

Reproductive suppression is relaxed when the breeding female is unable to shove colony mates effectively, such as when she is near parturition (Westlin et al. 1994), ill, or injured. If she dies, a few large nonbreeding females in the colony begin ovarian cycling within a week (Jarvis 1991a). They engage in shoving matches and then fights, which can result in serious wounds, especially on the face, thorax, and genital region, and sometimes lead to crippling or death (Jarvis 1991a; Lacey and Sherman 1991, 1997). After a new breeding female has physically dominated or neutralized rivals, fighting usually ceases, but the female's rate of shoving increases (Clarke and Faulkes 2001). Sometimes the dominant female continues to attack large female and male colony members (O'Riain 1996; van der Westhuizen 1997). Targeted males are mates of the former breeding female or close associates of other females (Clarke and Faulkes 2001; Lacey and Sherman 1997).

Replacement of breeding males and females from within colonies occurs in nature (Braude 1991a) and in captivity (Clarke and Faulkes 1998; Jarvis et al. 1991; Lacey and Sherman 1991, 1997). Breeding succession among males is determined by the mate choice(s) of the reproductive female rather than by physical combat among males (Clarke and Faulkes 1997; Lacey and Sherman 1991, 1997). Breeding males are among the highest-ranking, heaviest, and oldest males in their colony (Clarke and Faulkes 1998). Occasionally, a new breeding female will retain the previous breeding male or males (O'Riain 1996; van der Westhuizen 1997).

Size-based dominance hierarchies occur within colonies (Clarke and Faulkes 1998; Schieffelin and Sherman 1995). The largest individuals of both sexes, especially the breeders, obtain access to food or digging sites before the smaller colony mates. Intracolony disputes among nonbreeders over resources often involve jostling, shoving, and loud chirping but seldom are injurious.

Adult naked mole-rats often shove pups vigorously around the nest chamber (Lacey and Sherman 1991). Of 2,022 shoves of pups, 1,345 (66%) were by their mother, 482 (24%) by their father, and 195 (10%) by all nonbreeders combined (Stankowich and Sherman 2002). Shoving peaks when pups are 3–4 weeks old. Juveniles that were shoved as pups move away from disturbances more readily than juveniles that were isolated and not shoved (Stankowich and Sherman 2002). First-born litters in a new colony are shoved less than individuals from later litters (O'Riain 1996).

GENETICS. *Heterocephalus glaber* has $2n = 60$ chromosomes (George 1979). In the field, neighboring *H. glaber* colonies often are genetically similar, whereas geographically distant colonies are divergent (Bennett and Faulkes 2000; Faulkes et al. 1997a). Control region sequences of mitochondrial DNA (mtDNA) did not differ among 6 colonies from Mtito Andei, Kenya (Bennett and Faulkes 2000). However, haplotypes from Mtito Andei differed from those at Lerata, Kenya (400 km north) and Dembalawachu, Ethiopia (650 km north). Mean genetic divergence between Ethiopian and southern Kenyan haplotypes was 5.8% for the cytochrome-*b* gene (Bennett and Faulkes 2000). In captivity, naked mole-rats from northern and southern Kenya (sequence divergence, 3–4%) readily interbreed and produce healthy young. Analyses of blood proteins (Honeycutt et al. 1991b), DNA fingerprints (Faulkes et al. 1990c; Reeve et al. 1990), and mtDNA control region sequences (Bennett and Faulkes 2000; Faulkes et al. 1997a) indicate greater genetic homogeneity within than between colonies. Mean fingerprint band-sharing frequencies among colony members from 4 colonies captured near Mtito Andei were 0.92–0.99, average intracolony relatedness was 0.81, and the coefficient of inbreeding was 0.45 (Reeve et al. 1990).

CONSERVATION STATUS. The International Union for Conservation of Nature does not list *H. glaber* as threatened or endangered. However, given the patchy distribution of naked mole-rat colonies (Brett 1991a; Jarvis 1985) and their population genetic structure (Allard and Honeycutt 1992; Bennett and Faulkes 2000), extirpation of local, genetically distinct subpopulations is possible.

Naked mole-rats live in arid areas with little agriculture and minimal development. They are not a significant agricultural pest, although anecdotal reports suggest that naked mole-rats may have burrowed into underground storage granaries in Somalia. Expansion of the human population into parts of the *H. glaber* range will inevitably lead to conflict, especially because naked mole-rats relish casava and sweet potatoes, which are important agricultural crops.

Naked mole-rats are protected in several Kenyan Game Parks, including Tsavo, Kora, Meru, and Samburu. Their present distribution and conservation status in Ethiopia and Somalia are unknown. Procedures for maintaining naked mole-rats in captivity have been developed (Artwohl et al. 2002; Jarvis 1991b; Sherman and Jarvis 2002). Zoos worldwide exhibit naked mole-rat colonies in seminatural displays (e.g., Jarrow and Sherman 1996, 2001).

REMARKS. The generic name *Heterocephalus* refers to the animal's odd-looking head, whereas the specific epithet *glaber* refers to its smooth skin.

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