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Tachyoryctes macrocephalus.

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Tachyoryctes Rüppell, 1835

Tachyoryctes Rüppell 1835:35. Type species *Tachyoryctes splendens* Rüppell, by monotypy.

CONTEXT AND CONTENT. Order Rodentia, Infraorder Myomorpha, Family Rhizomyidae. The family consists of six species of myomorph mole-rats, four of which are confined to southeastern Asia. The African genus *Tachyoryctes* has been split between 21 forms in 14 full species (Allen, 1939), but currently only two species, *T. splendens* and *T. macrocephalus*, are recognized (Corbet and Hill, 1980; Honacki et al., 1982).

Tachyoryctes macrocephalus Rüppell, 1842

Giant Mole-rat

Tachyoryctes macrocephalus Rüppell 1842:97. Type locality "Schoa, Abyssinia," but probably not the modern province of Shoa (Yalden et al., 1976).

CONTEXT AND CONTENT. There are two valid subspecies (Yalden, 1975):

T. m. macrocephalus Rüppell, 1842, see above.

T. m. hecki Neumann and Rümmler, 1928:302. Type locality "Abakkara, about 150 km west of Lake Awasa, in the boundary region between Djamdjam and Arussi-Galla," but west is in error for east. Revised to Abakkara, south of Adaba, Ethiopia, ca 06°50′N, 39°15′E (Yalden et al., 1976).

DIAGNOSIS. The two African species of Rhizomyidae are readily distinguished by size. Adult weight of the smaller *T. splendens* is 160 to 280 g, and condylobasal length is 33 to 50 mm; *T. macrocephalus* weighs 300 to 1,000 g and has a skull 51 to 70 mm long. Rhizomyid mole-rats have 3/3 cheekteeth with a complex, hystricomorph-like crown pattern, in contrast to the 4/4 cheekteeth with simple crowns that characterize the Bathyergidae, the other family of African mole-rats.

GENERAL CHARACTERS. The giant mole-rat is a stocky, short-limbed rodent with a relatively large head and short tail (Fig. 1). The pelage is generally a pale brown color, with some slight variation to more ginger or more silver shades of brown, and paler ventrally. A conspicuous black patch occurs on the upper eyelid in life. Some individuals have a faint crown stripe. Eyes are large; external pinnae are visible but not conspicuous. The tail is whitish, thick at the base, and tapers sharply. Measurements (in mm) for adults are: head and body length, 210 to 313; tail length, 40 to 65; hindfoot length, without claws, 31 to 38; ear length 7 to 15 mm ($n = 10$; Yalden, 1975). Skull measurements ($\bar{X} \pm SD$) are: condylobasal length, 63.0 ± 4.5 (range 51.8 to 69.6); zygomatic breadth, 44.1 ± 3.3; interorbital width, 6.1 ± 0.3; upper incisor width, 13.6 ± 0.7; ($n = 12$ to 19, depending on breakage; Yalden, 1975).

DISTRIBUTION. *Tachyoryctes macrocephalus* is endemic to Ethiopia, where it is one of several vertebrate species restricted to high altitude grassland and moorland habitats. The subspecies *T. m. hecki* is reasonably well known; it occurs in a limited area of Balé Province, at altitudes of 3,200 to 4,150 m (Fig. 2; Corbet and Yalden, 1972; Dorst, 1972; Yalden, 1975; Yalden et al., 1976). The nominate race was ascribed by Rüppell (who did not, however, collect the specimens himself) to Shoa, but the then Kingdom of Shoa was not co-extensive with the modern province of that name. A locality in modern Wello or Begemdir is more likely. *T. m. hecki* occurs sympatrically with *T. splendens* in Balé Province, but *T. splendens* has a much wider range in Ethiopia and throughout higher ground in eastern Africa.

FIG. 1. External appearance of *Tachyoryctes macrocephalus* (photo by D. W. Yalden).

FOSSIL RECORD. The earliest rhizomyid fossils come from Miocene deposits, about 13 m.y.b.p., in Pakistan (Flynn, 1982). The earliest record of *Tachyoryctes* is from the Hadar Formation, Ethiopia, at about 3 m.y.b.p. (Sabatier, 1978); these fossils were described as a new species, *T. pliocaenicus*. The relationship of *T. pliocaenicus* to modern species has not been considered, and they have no phylogenetically useful fossil record.

FORM AND FUNCTION. *Tachyoryctes macrocephalus* shares with other mole-rats (Geomyidae, Spalacidae, Bathyergidae) a truncated skull with large incisors and rostrum; wide, strong, zygomatic arches; a broad occipital arch; and a relatively small braincase. The lower jaw has large incisors and the angular process is broad (Fig. 3). The interorbital region of the skull is both absolutely and relatively narrower than in *T. splendens*, so that the eyes are situated dorsally and close together.

The jaw muscles, especially the masseters, are large in many fossorial rodents, because digging often is performed chiefly with the incisors. Afework Bekele (1983*a*) compared *T. splendens* with *Rattus rattus*; the jaw muscles were respectively 4.17% and 2.09%

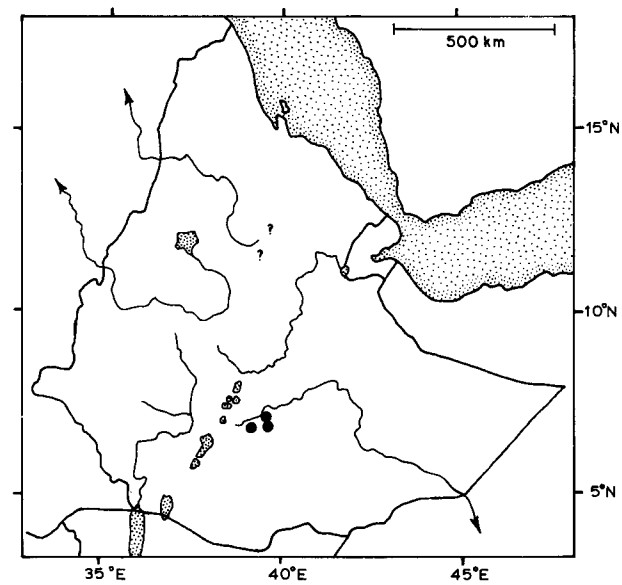

FIG. 2. Distribution of *Tachyoryctes macrocephalus* in Ethiopia (solid circles). Possible locations of nominate race are indicated by question marks (?).

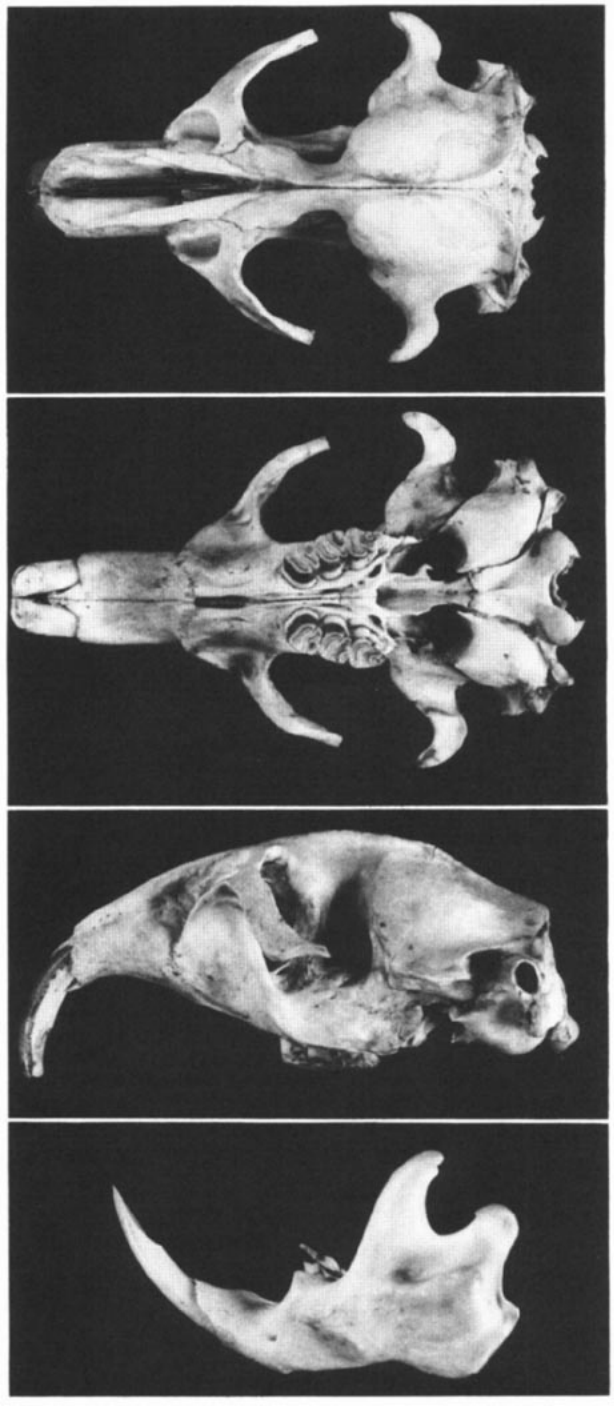

FIG. 3. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Tachyoryctes macrocephalus* (specimen N.H.M. A.A. 17484). Nasals are missing and zygomata are broken (photo by L. Lockey).

of the fresh body mass. For comparison, one large, 755-g *T. macrocephalus* which I dissected had jaw muscles 4.09% of its body mass, and in a younger animal, weighing 330 g, they were 3.38%. Thus, *T. macrocephalus* may be slightly less specialized than *T. splendens* for a fossorial life. The occipital musculature of *T. macrocephalus* was 1.69% and 1.33% of the body mass in the same two individuals, compared with 1.74% in *T. splendens* (Afework Bekele, 1983*b*).

Tachyoryctes presumably digs its tunnels with its incisor teeth, and can be observed to push earth out of the tunnel entrance with its head (Yalden, 1975). The incisors, although broad, are proportionately rather narrower than in *T. splendens*. The large, dorsally placed, eyes are presumably the principal sense organs for detecting predators.

ONTOGENY AND REPRODUCTION. Virtually nothing is known regarding reproduction and development. In *T. splendens*, litter size is usually one, sometimes two, rarely three or four (Rahm, 1971); there is a small amount of evidence, from the age structure of specimens in collections and in an observation colony, that the usual litter size in *T. macrocephalus* also may be only one (Yalden, 1975).

ECOLOGY. *Tachyoryctes macrocephalus* is a diurnal member of the high altitude Afroalpine moorland community, along with other endemic rodents such as *Arvicanthis blicki* and *Lophuromys melanonyx*. Other rodents in this community include the more nocturnal *Stenocephalemys albocaudata*, *L. flavopunctatus*, and *Otomys typus*, and also *T. splendens*. This community is typically present at altitudes above 3,700 m; below this, zones of giant heath, *Erica arborea*, and montane forest generally limit distribution of *T. macrocephalus*, but damp grasslands in river valleys extend down through the shrub and forest zones, allowing giant mole-rats to extend down to about 3,100 m (Dorst, 1972).

Tachyoryctes macrocephalus occupies a tunnel system 10 to 15 cm below ground level. The tunnels are about 12 to 15 cm in diameter, although the entrances are narrower (6 to 9 cm); one tunnel system, as excavated, was about 34 m long, apparently an essentially linear system with short side tunnels but no anastomoses. Tunnel systems apparently are occupied by a solitary individual. The presence of six adults in a small (0.11 ha) study area implies a density of 63/ha and a possible biomass of 33.6 kg/ha (Yalden, 1975).

Tachyoryctes macrocephalus feeds largely by collecting the herbage around a new tunnel entrance opened from below. After about 20 min of food gathering, the food supply is exhausted and the entrance is blocked from inside. Such plugged burrows, surrounded by a zone plucked of its vegetation, are characteristic of this species. Stomach analysis of six individuals suggested that grasses and dicotyledonous plants contributed equally to the diet, and that some individuals fed largely on roots (Yalden, 1975).

Known predators include the Abyssinian long-eared owl, *Asio abyssinicus*, recorded as taking a juvenile *T. macrocephalus* as well as *T. splendens* (Yalden, 1973), and the Simien fox, *Canis simensis* (Morris and Malcolm, 1977). The latter may be a major predator, as a limited sample of feces yielded the remains of 25 individual *T. macrocephalus*, representing about 47% by weight of the foxes' diet. Other potential predators in the area include *Buteo rufofuscus*, *Gypaetus barbatus*, and *Bubo capensis* among birds, and *Felis serval*, at least at lower altitudes. There appear to be no smaller predators in the area that could enter the burrow system (snakes, mustelids, or viverrids).

BEHAVIOR. The food-gathering behavior gives the impression of great nervousness; food is gathered in quick snatches, with the hindquarters remaining inside the burrow entrance. The animal retreats backwards into its burrow when disturbed or when a full load of food has been gathered (Yalden, 1975).

In the high altitude habitat of this species, severe frosts occur each night, at least during the dry season when skies are clear. Perhaps in response to this, most (possibly all) burrow entrances that have been used during the day are plugged from the inside in late afternoon. Activity appears to be restricted between about 0900 and 1730 h (dawn and dusk being 0630 and 1830 h at these latitudes).

Of activity visible at the surface, about 20% involved shovelling earth out of burrow entrances, 74% food gathering, and 6% observing the environment or the human observer. A colony of six adults, observed on 2 days for about 460 min each day, were active for about 170 min each day; this is about 6% of the theoretical maximum (Yalden, 1975).

Nothing is known of reproductive behavior, nor of any aspect of behavior underground.

REMARKS. Although *T. macrocephalus hecki* is abundant in the limited area of Balé Province where it is known to occur, the total potential range there is probably no more than 1,500 km^2 (Brown, 1969). The major ecological importance of *T. macrocephalus hecki* may be as a source of food for the Simien fox, an endangered species. A national park for the Balé Mountains has

been proposed, but not yet confirmed. The whereabouts of the nominate race, *T. m. macrocephalus* remains an enigma; the species does not occur in the well known Simien National Park. Rumors in 1974 that it may occur near Lalibela have still not been confirmed. The species is at present known from only 4 specimens of *T. m. macrocephalus* [in Frankfurt (2), London, and Berlin] and 20 specimens of *T. m. hecki* [in Berlin (type), Paris (4), London (13), and Addis Ababa (2)].

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