

Otomys angoniensis. By G. N. Bronner and J. A. J. Meester

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***Otomys angoniensis* Wroughton, 1906**

Angoni Vlei Rat

Otomys irroratus angoniensis Wroughton, 1906:274. Type locality M'Kombhuie, Angoniland (2,438 m), Malawi.

Otomys angoniensis: Osgood (1910:10). First use of specific name combination.

Otomys divinatorum Thomas, 1910:311. Type locality Rombo, Mt. Kilimanjaro (1,616 m), Tanzania.

Otomys rowleyi Thomas, 1918:209. Type locality Coguno, Inhambane, Mozambique.

Otomys mashona Thomas, 1918:210. Type locality Mazoe, Mashonaland (1,219 m), northeastern Zimbabwe.

Otomys tugelensis Roberts, 1929:113. Type locality Klipspruit, Utrecht, northern Natal.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorphi, Infraorder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Otomyinae. *Otomys angoniensis* has been included in the Otomyidae (Roberts, 1951), Nesomyidae (Chaline et al., 1977) and Cricetidae (Allen, 1939; de Graaff, 1981; Honacki et al., 1982; Misonne, 1974; Smithers, 1983). Ellerman (1941), Carleton (1984) and Meester et al. (1986), like Tullberg (1899), classified all southern African muroids as subfamilies within the Muridae, an approach adopted here. Seven subspecies of *O. angoniensis* currently are recognized (Meester et al., 1986).

O. a. angoniensis Wroughton, 1906:274, see above (*nyikae* Wroughton, 1906:276 is a synonym).

O. a. canescens Osgood, 1910:10. Type locality Kijabe, Kenya.

O. a. divinatorum Thomas, 1910:311, see above.

O. a. elassodon Osgood, 1910:10. Type locality Naivasha, Kenya.

O. a. maximus Roberts, 1924:70. Type locality Machile River (tributary to Zambezi River), southwestern Zambia. (*davisi* Lundholm, 1955:295 is a synonym.) Regarded as a distinct species by Roberts (1951), Smithers (1983) and Swanepoel et al. (1980).

O. a. rowleyi Thomas, 1918:209, see above (*mashona* Thomas 1918:210 is a synonym).

O. a. tugelensis Roberts, 1929:113, see above (*sabiensis* Roberts, 1929:114 and *pretoriae* Roberts, 1929:114 are synonyms).

DIAGNOSIS. Nasal bones expanded anteriorly (conspicuously so in *O. a. angoniensis*, and *O. a. divinatorum*) and narrower posteriorly, with a gradual angular transition between these regions; interorbital region trumpet- or spoon-shaped (Fig. 1); petrotympanic foramen (situated on the posterointernal surface of the bulla) small and slitlike, and in a shallow depression that extends obliquely anterolaterad (Fig. 2). Lower incisors each with one deep outer and one shallow inner labial groove; molars with a pronounced laminate configuration; four laminae on ml, and five to eight (usually seven) on M3. Baculum spatulate basally with a central raised portion in ventral view (Fig. 3); greatest length of the proximal portion, 4.4 mm (3.9 to 4.9); greatest width, 0.97 mm (0.7 to 1.2; Davis, 1973).

Otomys angoniensis and its sibling species *O. irroratus* (Davis, 1962; Misonne, 1974) often are confused. Although the two species sometimes may be differentiated on the basis of color and size (*O. irroratus* is darker and larger), these characters vary geographically (de Graaff, 1981). Hind foot length (with claw) and breadth differ distinctly between the two species at one locality in the Transvaal (Davis, 1973), but over a wider area in the Transvaal (Rautenbach, 1982), and in Zimbabwe (Smithers, 1983), these features overlap. Davis (1973) reported that in *O. angoniensis* a ring of orange-buffy hair about 2 mm wide surrounds the eye, whereas in *O. irroratus* it is absent; however, this character is not constant in *O. angoniensis*. Davis (1973) also found baculum size and shape to differ significantly between the two species, but the constancy of this difference requires

confirmation. The most reliable criterion for differentiating between these species is the shape of the petrotympanic foramen, which is large and rounded in *O. irroratus*, and small and slitlike in *O. angoniensis* (Fig. 2).

Otomys denti, *O. sloggetti*, and *O. unisulcatus* differ from *O.*

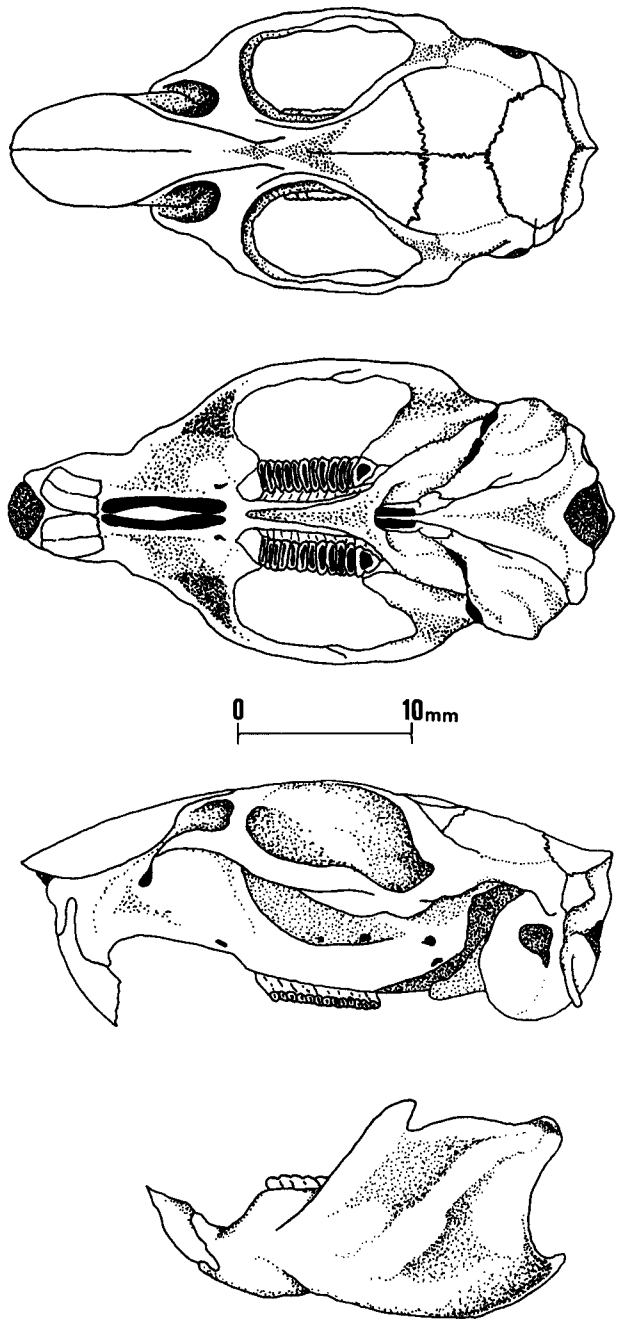


FIG. 1. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Otomys angoniensis tugelensis*, female, Durban, South Africa.

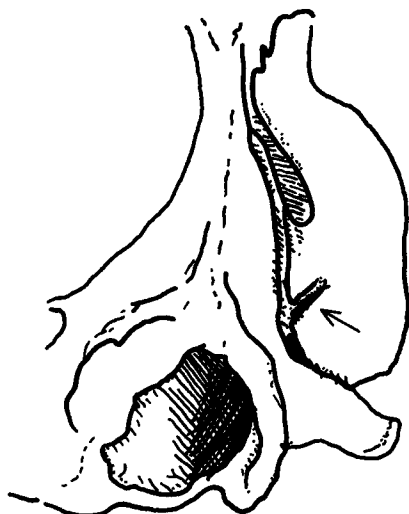


FIG. 2. Basicranial region of *Otomys angoniensis* showing the slitlike petrotympanic foramen (from Misonne, 1974).

angoniensis in having only one labial groove on each lower incisor; *O. typus* differs in having two deep grooves on each lower incisor. *O. laminatus* and *O. angoniensis* can be differentiated according to the number of laminae on M3, there being nine to 10 in the former and five to eight in the latter. *O. angoniensis* and *O. anchietae* both have five to eight laminae on M3, but the former has only four laminae on m1, whereas the latter has five, and a rounded petrotympanic foramen.

GENERAL CHARACTERS. Body size moderate to large (compared with other muroids), with a stocky physique, blunt face, medium-sized eyes, and medium-sized, rounded, and well-haired pinnae (Fig. 4). Means, ranges (in parentheses), and sample sizes for body measurements (in mm) of Pan-African specimens sampled at the Transvaal Museum (South Africa) are as follows: head and body length, 155 (105 to 207) $n = 116$; tail length, 86 (43 to 131) $n = 117$; hind foot length, 26 (19 to 39) $n = 116$; ear length, 20 (9 to 30) $n = 116$. Sexual differences in body dimensions are not significant at $P = 0.05$. Mean body measurements (in mm) for Transvaal males and females, respectively, are as follows: head and body length 138 ($n = 91$), 144 ($n = 97$); tail length 79 ($n = 91$), 79 ($n = 97$); hind foot length 26 ($n = 91$), 25 ($n = 97$); ear length 19 ($n = 91$), 20 ($n = 96$; Rautenbach, 1982). Mean mass of males in the Transvaal is 89.9 g (25 to 138 g; $n = 56$) and that of females 96.6 g (47 to 216 g; $n = 56$; Rautenbach, 1982).

Otomys angoniensis varies markedly in size, and includes a large subspecies (*O. a. maximus*) in Angola (Misonne, 1974; Smithers, 1983). Means, ranges (in parentheses) and sample sizes of body measurements (in mm) of *O. a. maximus* (based on specimens in the Transvaal Museum) are as follows: head and body length, 183 (154 to 207) $n = 17$; tail length, 110 (81 to 131) $n = 17$; hind foot length, 34 (29 to 39) $n = 16$; ear length, 23 (20 to 30) $n = 16$. Male and female measurements do not differ significantly at the 5% level. Mean mass of 178.4 g (112 to 242 g; $n = 11$) in males and 205.3 g (140 to 255 g; $n = 5$) in females was reported by Smithers (1971).

Head and body length of *O. a. classodon* from Kenya also is greater than that of the other subspecies except *O. a. maximus*. Means, ranges (in parentheses) and sample sizes for body measurements (in mm) are as follows: head and body, 172 (141 to 189) $n = 12$; tail length, 80 (65 to 91) $n = 12$; hind foot length, 26 (20 to 28) $n = 12$; ear length, 22 (20 to 26) $n = 12$.

On the basis of measurements of types, *O. a. rowleyi*, *O. a. angoniensis*, *O. a. canescens*, *O. a. tugelensis*, and *O. a. divinatorum* are of similar size. The tail is short in all subspecies, usually between 50% and 60% of head and body length. Hind foot length ranges from 19 to 35 mm in all except *O. a. maximus* in which the observed range is 29 to 42 mm (Rautenbach, 1982; Smithers, 1971; Smithers and Wilson, 1979).

Means, ranges (in parentheses) and sample sizes for selected skull measurements (in mm) of *O. angoniensis* are as follows: greatest length of skull, 37.5 (26.3 to 49.1) $n = 105$; condylobasal length,

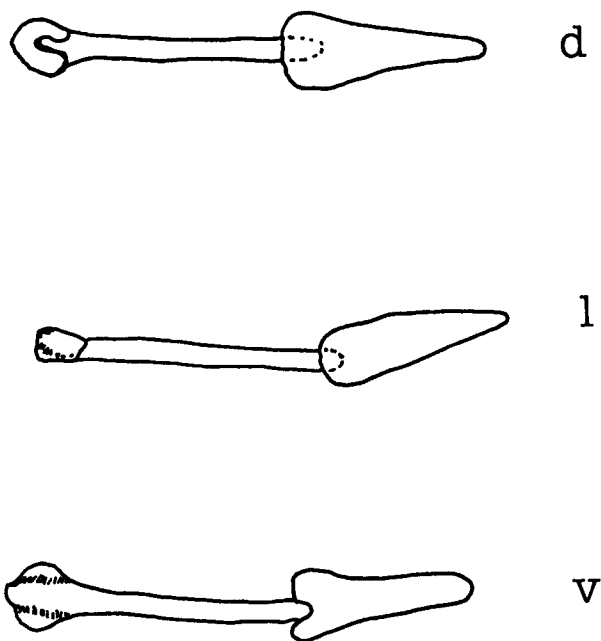


FIG. 3. Dorsal (d), lateral (l), and ventral (v) views of the baculum of *Otomys angoniensis* (from Davis, 1973).

37.2 (25.4 to 49.9) $n = 105$; condylobasilar length, 32.8 (22.5 to 42.3) $n = 107$; basal length, 35.0 (23.2 to 46.9) $n = 104$; basilar length, 30.2 (20.2 to 42.1) $n = 106$; greatest zygomatic breadth, 18.9 (16.1 to 23.4) $n = 104$; greatest length of nasals, 16.0 (10.2 to 21.8) $n = 106$; greatest width across nasals, 7.1 (4.7 to 9.5) $n = 108$; interorbital constriction (smallest width across nasals), 1.8 (1.1 to 2.64) $n = 105$; greatest width of braincase, 14.2 (11.8 to 16.0) $n = 108$; palatal length, 22.8 (16.5 to 30.3) $n = 107$; palatilar length, 17.5 (13.5 to 22.4) $n = 106$; greatest length of palatal foramina, 6.6 (4.1 to 8.7) $n = 104$; length of maxillary toothrow at alveolar rim, 9.2 (7.8 to 11.5) $n = 101$.

Fur long and soft. Dorsal color gray to reddish to brown, coarsely tinged with buff; individual hairs slaty-black basally with an annulation of buff distally; hair tips buffy or dark. Buffy-orange patches often occur in nostril and throat regions (de Graaff, 1981; Smithers, 1983). Ventral color generally a dull, dark gray. Tail moderately haired (less so in *O. a. rowleyi*), unpencilled and bicolored, dark above and buffy-white below. Color varies geographically: *O. a. angoniensis* generally darkest, with least gray in pelage; *O. a. divinatorum* usually palest and grayest. Black-tipped hairs are most numerous in *O. a. maximus* (Lundholm, 1955); venter of *O. a. canescens* contains more buff than that of other subspecies.

Both surfaces of all feet a uniform purple-black color; upper surfaces well haired; palmar and plantar surfaces naked. Forearms and thighs resemble upper parts. Pollex and outermost digits of the hind feet reduced in size. All digits clawed; hind claws longer than those on the forefeet.

DISTRIBUTION. The range of *O. angoniensis* includes southern savanna woodlands and grasslands from the northeastern Cape Province, South Africa, to Angola in the west and Kenya in the east (Fig. 4; Davis, 1962, 1974; de Graaff, 1981; Smithers, 1983). Three subspecies occur in southern Africa: *O. a. maximus* in southwestern Angola, Caprivi, Okavango, and southwestern Zambia (Smithers, 1971); *O. a. tugelensis* in Natal, Transvaal, and extreme northeastern Cape (Meester et al., 1986; Rautenbach, 1982); and *O. a. rowleyi* in northeastern Transvaal, Zimbabwe and Mozambique (Smithers and Lobao Tello, 1976; Smithers and Wilson, 1979). Distribution records for the east African subspecies are scarce, making delimitation of subspecific ranges speculative. *O. a. angoniensis* occurs in Malawi, and possibly also in central western Mozambique, whereas *O. a. divinatorum* occurs in central and northern Tanzania. *O. a. canescens* and *O. a. classodon* occur in southern and central Kenya.

FOSSIL RECORD. Although *Otomys* is predominant among rodents in Pleistocene deposits in southern Africa, *O. angoniensis*

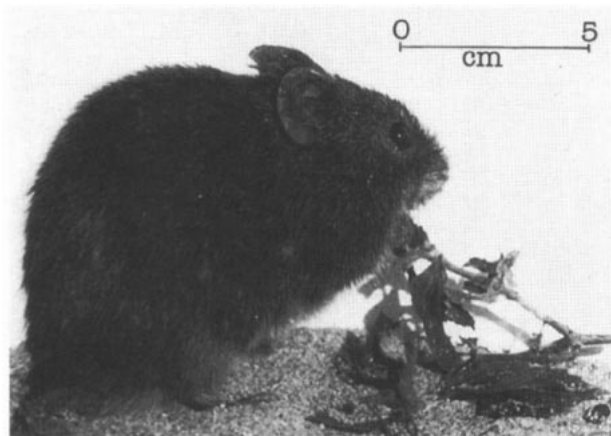


FIG. 4. Male *Otomys angoniensis tugelensis* from Durban, Natal, South Africa (photograph by G. Bronner).

is not represented (de Graaff, 1961). Fossils from the late Pliocene of South Africa and the late Pleistocene of east Africa were described as *Palaeotomys* (Broom, 1937), while another genus (*Protomys*) was recorded from the late Pliocene of South Africa (Broom and Schepers, 1946; Lavocat, 1978). *Euryotomys*, described by Pocock (1976) from early Pliocene deposits in South Africa, has one deep outer and one shallow inner groove on each upper incisor; molars with a laminate configuration, but which retain traces of cuspidation; and enlarged M3 showing multiplication of laminae. On the basis of these features, Pocock (1976) referred *Euryotomys* to the Murinae; suggested that *Otomys* and *Rhodomys* are closely related through the intermediate *Pelomys*; and speculated that otomyines must have descended from a *Pelomys*-like murine with grooved upper incisors within the past 4 to 5 million years. Thus, he implied that incisor grooving is plesiomorphic in the Otomyinae. Conversely, Carleton and Musser (1984) argued that ungrooved incisors may be plesiomorphic in the Otomyinae, consistent with the plain incisors and more simple molar pattern of *Parotomys*. If so, then *Euryotomys* could justifiably be assigned to the Otomyinae, which would extend the known geologic age of this taxon to the early Pliocene.

FORM AND FUNCTION. Pelage shaggy. Individual hairs narrow basally, increase in width to the distal third, then taper gradually to a long, fine tip (Keogh, 1985). Guard hairs grooved for their distal half, with a lanceolate-pectinate cuticular scale pattern basally that slowly flattens to become an irregular wavy-mosaic pattern distally. Mean length ($\pm SD$) of grooved guard hairs 15.9 ± 0.99 mm, and that of ungrooved hairs 13.97 ± 1.37 mm (Keogh, 1985). Moulting patterns are not known.

Skull stout and arched (Fig. 1). Interparietal large with a square or trapezoid shape. Supraorbital ridges prominent. The transition between the broad anterior and narrower posterior nasal regions forms a gradual angle, the acuteness of which varies subspecifically. Zygomatic stout, each with an expanded middle section; zygomatic spines and notches moderately to strongly developed. Postglenoid fossa extensive such that only a narrow strut of the squamosal remains above the otic capsule. Pterygoid fossa moderately to deeply excavated; mesopterygoid fossa long and projects between the third molars. Bony palate narrow with deep furrows and a high median keel. Incisive foramina narrow and about as long as the diastema. A strut of the alisphenoid separates the masticatory foramen from the accessory foramen ovale. Mandibular foramina deep and coronoid processes small. Compared with other murids, the mastoid bulla is moderately enlarged; the tympanic bulla is medium to large with a globose form. Malleus of murine conformation; stapedial foramen inconspicuous (Carleton and Musser, 1984; Cockerell et al., 1914; Davis, 1973; de Graaff, 1981; Ellerman, 1941; Roberts, 1951).

The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16. Incisors are broad and opisthodont with labial surfaces pigmented yellow. Molars are laminate and hypselodont, but not hypselodont. M3 has multiple rootlets, and is larger than M1 or M2. Transverse molar laminae are tightly packed with no apparent indication of cuspidation; the molar lamina formula is $3-2-(5\ \text{to}\ 8)/4-2-2$. Upper toothrows converge anteriorly and have a marked laterad slant

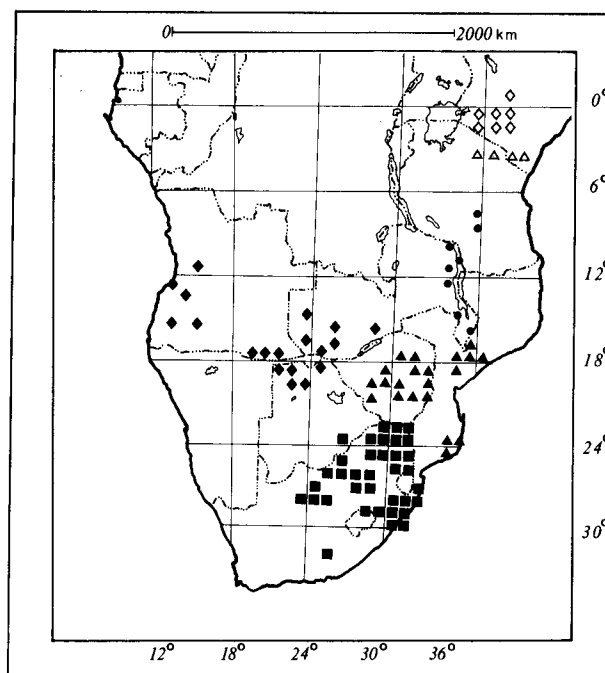


FIG. 5. Geographical distribution of *Otomys angoniensis*, plotted in 1° squares. Subspecies are: (●) *O. a. angoniensis*; (△) *O. a. divinorum*; (◇) *O. a. canescens* and *O. a. elassodon*; (◆) *O. a. maximus*; (▲) *O. a. rowleyi*; and (■) *O. a. tugelensis*.

(Carleton and Musser, 1984; Davis, 1973; de Graaff, 1981; Ellerman, 1941).

The hindgut of *O. angoniensis* is specialized for herbivory (Perrin and Curtis, 1980). Although the stomach is simple (with only a small, yet elastic, band of cornified epithelium), the intestine is long and spiralled. The caecum is large and complex, with a papillose lining and 32 haustra arranged in double rows along the greater curvature from the ileum to its blind end. A gall bladder is lacking. Caecal fermentation and vitamin metabolism presumably are facilitated by coprophagy that occurs in this species.

ONTOGENY AND REPRODUCTION. The reproductive biology of *O. angoniensis* is not well known. Powell's (1925) report that individuals begin breeding at 4 months of age, that they breed thrice annually, and that litter size ranges from three to five, probably refers to *O. angoniensis* and *O. irroratus* together.

Otomys angoniensis is seasonally polyoestrous. In southern Africa, pregnant and lactating females have been captured between August and May, whereas juveniles have been recorded only in spring and summer (September to January). No gravid females have been captured in the dry early and midwinter months (Rautenbach, 1982; Smithers, 1971; Smithers and Wilson, 1979). Breeding evidently peaks in the wet summer months and declines in the dry winter when food availability decreases. There is not, however, always a distinct break in breeding, as shown by the collection of three well-developed embryos in August (late winter; Pienaar et al., 1980).

The reproductive pattern of *O. angoniensis* resembles that of its sibling species *O. irroratus*, in which breeding activity slows or ceases in early winter, then increases to former levels in late winter (Davis and Meester, 1981). The resumption of high levels of breeding in *O. irroratus* corresponds with an increase in photoperiod, even though food quality and quantity are poorest at this time (Davis and Meester, 1981). The same may apply in *O. angoniensis* in southern Africa.

Otomys angoniensis in the tropical highlands of Kenya is iteroparous, but breeding peaks in the wet months (April to September) when the vegetation is most lush (Taylor and Green, 1976). Seemingly, rainfall acts via the vegetation to govern the timing and intensity of reproduction in the tropics where little seasonal variation in photoperiod or temperature occurs.

Only one birth in captivity has been reported for *O. angoniensis*, hence information on gestation periods, litter sizes, and the appearance and postnatal development of young is unavailable. In

Kenya, in utero litter sizes range from one to five, with a mean of 2.80 ($n = 109$; Taylor and Green, 1976). Females were captured with two to four (usually three) embryos in Namibia (Shortridge, 1934); three to five in Botswana ($\bar{X} = 3.7$; Smithers, 1971); two to three in Zambia (Ansell, 1960, 1964); three in the Kruger National Park (Pienaar et al., 1980); one to three in Malawi (Hanney, 1965) and two to five embryos in the Transvaal ($\bar{X} = 2.9$; $n = 14$; Rautenbach, 1982). Evidently, litter size ranges from one to five, most often two to three. No regular pattern of implantation in the uterine horns can be discerned (Rautenbach, 1982; Smithers, 1971).

Young are precocial at birth, with a dense, buffy-colored pelage, and erupted incisors that enable them to cling to the mother's nipples (Ansell, 1960). Pups are suckled on two pairs of inguinal mammae. Young born in captivity may be consumed by their mother, especially if she is stressed.

ECOLOGY. Angoni vlei rats are terrestrial and cursorial, and occupy coastal, montane, and submontane grasslands; southern savanna grasslands; and woodlands, generally at elevations below 2,500 m (Ansell, 1960, 1964; Hanney, 1965; Misonne, 1974; Rautenbach, 1982). Within their range their distribution is patchy, mainly because of their requirement for mesic habitats (Smithers and Lobao Tello, 1976). This species is associated closely with dense vegetation (reedbeds, dense stands of sedges and semi-aquatic grasses) in low-lying wet areas, such as in swamps and along the fringes of vleis (hollows in which water collects during the rainy season), rivers, and streams (Rautenbach, 1982; Smithers, 1971, 1983). It is not, however, completely restricted to such habitats and sometimes inhabits drier grasslands considerable distances from water (Rautenbach, 1982). *O. a. rowleyi* moves into drier habitats in the wet season (Smithers and Lobao Tello, 1976), suggesting seasonal variation in home range. Hanney (1965), however, commented that the concept of home range may not be applicable to this species.

Where *O. angoniensis* coexists with *O. irroratus* (mainly on the Transvaal highveld of South Africa), it generally inhabits more xeric microhabitats than the latter species (Davis, 1962; Roberts, 1951) although both species may use the same runway systems (Misonne, 1974).

In Zambia, *O. angoniensis* is usually plentiful wherever it occurs (Ansell, 1960); in Malawi it may be the dominant small mammal species (in terms of biomass) in many montane habitats experiencing high rainfall (Hanney, 1965). However, Davis (1973) argued that this speaks more for the size of *O. angoniensis* than for its numbers, and Taylor and Green (1976) recorded only moderate (30 individuals/ha), but stable, population densities in the Kenyan highlands.

Davis (1973) found a statistically significant association between the distribution of *O. a. tugelensis* and several plant species, including *Helictotrichon turgidulum*, *Cynodon dactylon*, *Melilotus alba*, *Hyparrhenia dregeana*, *Berkheya radula*, *Chironia palustris*, and *Conyza podocephala*, on a study grid near Pretoria, South Africa. These plants were, conversely, negatively associated with the presence of *O. irroratus*, which instead was associated closely with plants providing denser basal and canopy cover. Population size of *O. angoniensis* is regulated by the availability of cover, and effective removal of cover results in the depletion of populations, mainly because of emigration and increased predation (Green and Taylor, 1975).

The diet is strictly herbivorous, consisting of an array of grasses, newly sprouting reeds (*Phragmites* sp.) and the rhizomes and roots of reeds (de Graaff, 1981; Smithers, 1983; Smithers and Wilson, 1979). Taylor and Green (1976) found 77% to 87% of the diet was composed of stems and leaves of grasses and other monocotyledonous plants. Stems are bitten off near the ground, then manipulated with the forefeet whilst the animal sits on its haunches. Small pieces (to 5 cm long) are bitten off and eaten; coarser stem material is discarded as small piles of cuttings along their trails (Smithers, 1983; Smithers and Wilson, 1979). In Kenya, *O. angoniensis* ingests more dicotyledonous material in the dry months, and occasionally also eats the bark of shrubs and trees (such as *Lantana* and *Eucalyptus*; Taylor and Green, 1976). At some localities, it is granivorous, and consumes millet seed put out to feed ducks (Anatidae; Smithers, 1971), or wheat (Taylor and Green, 1976). In captivity, Angoni vlei rats eat large quantities of lettuce, carrots, and maize seeds, but seem to prefer succulent, freshly-picked grasses. Infrequently, mouse cubes and mealworms also may be consumed.

The flesh of *O. angoniensis* is attractive to other rodents and

to shrews (Soricinae) that readily scavenge bodies of individuals caught in traps (Smithers, 1971). In Botswana, *O. a. maximus* is captured and eaten in large numbers by tribesmen during the annual burning of the reedbeds (Shortridge, 1934). This species also is eaten by puffadders (*Bitis arietans*), and the remains of an *Otomys*—probably *O. angoniensis* according to Davis (1973)—were recorded in stomach contents of a black mamba (*Dendroaspis polylepis*; Dixon, 1966). Owls, small felids and viverrids, however, are the main predators of *O. angoniensis*. Percentage occurrence of this species in owl pellets at Barberspan (Transvaal) ranged from 48.3% in the grass owl (*Tyto capensis*), to 17.0% in the marsh owl (*Asio capensis*); 12.2% in the barn owl (*Tyto alba*); and 5.3% in the spotted eagle owl (*Bubo africanus*; calculated from data in Dean, 1978). Other avian predators include the black-shouldered kite (*Elanus caeruleus*; Davis, 1973). The percentage occurrence of *O. angoniensis* in stomach items of carnivores ranged from 42% in the serval (*Felis serval*) to 37% in the large gray mongoose (*Herpestes ichneumon*); 14% in the African wild cat (*Felis lybica*); 11% in the civet (*Civettictis civetta*); 10% in the water mongoose (*Atelax paludinosus*); and 4% in the small-spotted genet (*Genetta tigrina*; Smithers, 1971, 1983; Smithers and Wilson, 1979). *O. angoniensis* also is eaten by the black-backed jackal (*Canis mesomelas*) and the side-striped jackal (*C. adustus*), but composes less than 5% of their respective diets (Smithers, 1983).

Parasites of *O. angoniensis* include fleas: Pucilidae—*Xenopsylla hipponax*, *X. versuta*, and *X. brasiliensis* (de Graaff, 1981); Hystrichopsyllidae—*Ctenophthalmus acanthurus*, *C. evidens*, *C. calceatus*, *C. eumeces*, *Dinopsyllus ellobius*, *D. longifrons*, *D. lypusus*, *Listropsylla fouriei*, and *L. prominens* (de Graaff, 1981; Hanney, 1965); and Chimaeropsyllidae—*Chiastopsylla rossi* (Zumpt, 1966). The well-known parasite groups such as mites, chiggers, flatworms, and roundworms are poorly known for this species (de Graaff, 1981). Mites include *Laelaps transvaalensis* and *Androlaelaps dasymys* (Davis, 1973). The only parasitic louse recorded is *Polyplax otomydis*, and ticks include: *Haemaphysalis leachii* (immatures); *Ixodes thomasa* (adults); *Rhipicephalus hurti* (immatures); and *R. capensis* (Davis, 1973; de Graaff, 1981). Davis (1973) recorded the infestation of Angoni vlei rats by two species of chiggers (larval trombiculids), namely *Euschoengastia africana* and *E. otomyia*. In Kenya, *O. angoniensis* is a reservoir host for various rickettsial pathogens, including *Rickettsia conorii* (tick-borne) and *R. prowazekii* (louse-borne; Heish, 1957; Heish and Harvey, 1959). Two species of filaria also were reported from *O. angoniensis* in Kenya (Nelson et al., 1962). Nematode parasites include *Longistriata capensis* and *Paranoplocephala omphalodes* (Davis, 1973). In both southern Africa and Kenya, *O. angoniensis* was infected with bilharzia (*Schistosoma haematobium*, *S. mansoni*, and *S. mattheei*; Pitchford, 1959; Pitchford and Visser, 1962), and harbored the schizomycete *Pseudomonas pseudomallei* that causes melioidosis (de Graaff, 1981). Roberts (1939) recorded several rodent "die-offs" in Kenya involving *O. angoniensis*, and commented that disease might play a role in regulating population density.

The pucilid fleas carried by *O. angoniensis* are principal vectors of plague bacilli (*Pasteurella pestis*; de Graaff, 1981). Angoni vlei rats thus are regarded as intermediary hosts to this pathogen, the principal reservoirs being gerbils (*Tatera*). Recently, another pathogenic bacterium (*Acinetobacter lwoffii*) was isolated (Shepherd and Leman, 1985). Because *O. angoniensis* rarely comes into contact with humans, it is unlikely to serve as a direct vector for disease transmission to man. However, it may act as a link in the transmission of several pathogens from their reservoir hosts to rodents that are commensal with man, such as *Mastomys natalensis* and *M. coucha*.

BEHAVIOR. Angoni vlei rats are antisocial and solitary, but individuals congregate near vleis and bodies of permanent water (Shortridge, 1934), where they may occur in pairs or small family parties (Smithers, 1983). Sleeping and breeding occur in dome-shaped nests of shredded vegetation situated below dense canopies, usually in clumps of grass (Smithers, 1983) or in burrows. Although *O. angoniensis* in Malawi does not burrow (Kershaw, 1922), in Kenya and Namibia it usually burrows unless the substrate is too moist for excavation (Green and Taylor, 1975; Shortridge, 1934), and captive *O. a. tugelensis* dig their own burrows (Davis, 1973).

Otomys angoniensis is active year-round, but daily activity varies both seasonally and geographically (Shortridge, 1934). Activity is mainly diurnal (Ansell, 1960; Smithers, 1983), except in Zimbabwe and Botswana where it is predominantly nocturnal (Choate,

1972; Smithers, 1971). Nocturnality at several localities in South Africa has indicated owl predation and Davis (1973) commented that its activity patterns correspond closely to those of the primarily crepuscular *O. irroratus*.

Movements occur along intricate, well-defined runway systems through and under the vegetation. These runs may be inundated with water in more mesic habitats, and often also are used by several other coexisting rodents (such as *Mastomys natalensis*, *M. coucha*, and *Rhabdomys pumilio*) and insectivores (such as *Crocidura flavescens*; Davis, 1973). *O. angoniensis* is trap shy, and enters traps (probably by accident) only if these are placed in runways (Davis, 1973; Taylor and Green, 1976). It is not a good swimmer, but readily enters shallow water to cross from one reedbed to another (Rautenbach, 1982; Shortridge, 1934).

Defecation occurs at any time during walking and feeding; scattered piles of feces are deposited along runways and near food plants. In captivity, large quantities of solid wastes not reingested also are produced, and are deposited indiscriminately in the cages.

GENETICS. Both the diploid chromosome number and the fundamental number are 56, the karyotype comprising 28 pairs of acrocentric chromosomes (Matthey, 1964). This contrasts with $2n = 28$ and $NF = 50$ in *O. irroratus*. Karyotypic differences between the two species are not the result of polyploidy (Matthey, 1964).

Some melanistic *O. angoniensis* specimens (with light buffy dorsal and ventral coloration) are stored at the Transvaal Museum (South Africa), but the genetic basis of this melanism has not been investigated.

REMARKS. Lundholm (1955), Roberts (1951), Smithers (1983) and Swanepoel et al. (1980) regarded *O. a. maximus* as a distinct species on the basis of size differences. The size differences, however, are not absolute, and mean ($\bar{X} \pm 3SD$) for the two taxa overlap broadly, so no more than subspecific separation is justified.

Otomys angoniensis canescens and *O. a. elassodon* may be synonymous. Both taxa were described by Osgood (1910) from localities on the Kinangop Plateau, Kenya, only 30 km apart. Osgood (1910) differentiated between them using color, skull profile, and molar width. In view of the infraspecific size and color variation in *O. angoniensis*, and the close proximity of the type localities of *O. a. canescens* and *O. a. elassodon*, the basis of this differentiation is suspect.

A taxonomic review of *O. angoniensis* incorporating morphometric, cytological, and distribution data is required to clarify subspecific relationships. Available information on reproduction, behavior, and habits is meager, and more data are needed for a coherent understanding of the natural history of this species.

The generic name *Otomys* is derived from the Greek *otos* = ear and *mys* = mouse, referring to the large and conspicuous ears of these rats. The specific name refers to the type locality (Angoniland).

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