

Aethomys ineptus (Rodentia: Muridae)

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Abstract: *Aethomys ineptus* (Thomas and Wroughton, 1908), commonly called the Tete veld rat, is a medium-sized rodent with a long, sparsely haired tail and spermatozoa with spatulate-shaped heads (unique for all muroid rodents thus far examined). *A. ineptus* co-occurs with its sibling species, *A. chrysophilus*, and in areas of co-occurrence, an examination of spermatozoa, diploid number, allozymes, or mitochondrial DNA is required to distinguish the 2. Previous work described as many as 11 species of *Aethomys*, but recent evidence indicates a need for taxonomic revision of the genus. Endemic to Africa, *A. ineptus* prefers habitats where there is substantial cover in the form of shrubs, rocks, and herbaceous vegetation. It is not of special conservation concern. DOI: 10.1644/809.1.

Key words: *Aethomys*, Africa, muroid, rodent, sibling species, Tete veld, Tete veld rat

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Aethomys ineptus (Thomas and Wroughton, 1908) Tete Veld Rat

Mus chrysophilus ineptus Thomas and Wroughton, 1908:546.

Type locality “Tete, Zambezi River, Mozambique.”

Mus chrysophilus tzaneenensis Jameson, 1909:460. Type locality “Tzaneen, north-eastern Transvaal [= Limpopo Province], South Africa.”

Mus chrysophilus pretoriae Roberts, 1913:85. Type locality “Fountains Valley, Pretoria, Transvaal [= Gauteng Province], South Africa.”

Aethomys chrysophilus magalakuini Roberts, 1926:254. Type locality “Wilhanshohe, Magalakuin [= Mogalakwena] River, north-western Transvaal [= Limpopo Province], South Africa.”

Aethomys chrysophilus capricornis Roberts, 1926:254. Type locality “Newgate Farm, Soutpansberg, northern Transvaal [= Limpopo Province], South Africa.”

Aethomys chrysophilus tongensis Roberts, 1931:235. Type locality Mangusi Forest, north-eastern Zululand [= Kwa-Zulu-Natal Province], South Africa.”

Aethomys chrysophilus ineptus G. M. Allen, 1939:369. Name combination.

Aethomys chrysophilus fouriei Roberts, 1946:319. Type locality “Oshikanga, Ovambo-Angola border” [Namibia].

Aethomys chrysophilus harei Roberts, 1946:320. Type locality “Waterberg, Otjiwarongo district, South-West Africa” [north-central Namibia].

Aethomys ineptus: Chimimba, 1998:432. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Muridae, subfamily Murinae, genus *Aethomys* (Bronner et al. 2003). The recognition of *A. ineptus* is based on a taxonomic elevation of 1 of the 10 previously recognized subspecies of *A.*

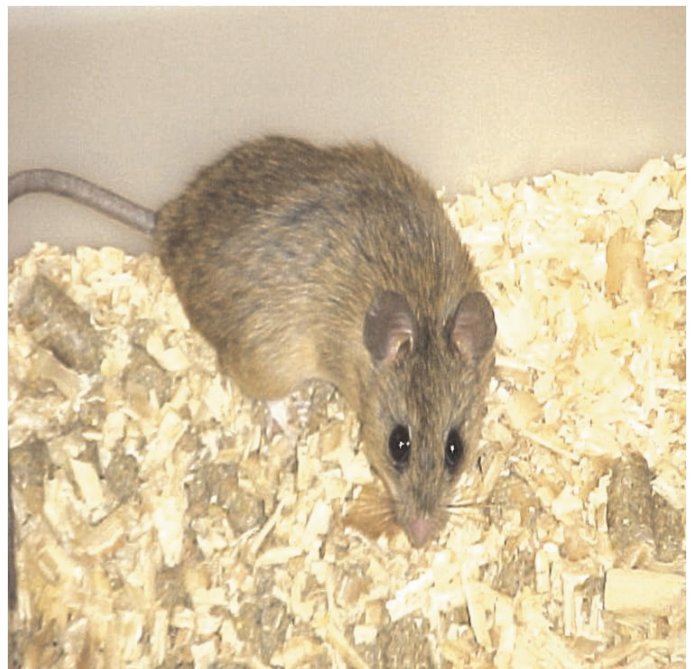


Fig. 1.—Adult *Aethomys ineptus* from Ezemvelo Nature Reserve, Mpumalanga Province, South Africa. Photographed in captivity by S. P. Muteka.

chrysophilus (sensu lato) in a recent revision of the genus in southern Africa (Chimimba 1998; Chimimba and Bennett 2005; Chimimba et al. 1999). Seven of the 9 previously recognized subspecies were reallocated to *A. ineptus* as junior synonyms (Chimimba et al. 1999—see synonyms above). Although a subsequent infraspecific morphometric analysis of *A. ineptus* from southern Africa (Chimimba 2001) suggested a longitudinal clinal pattern of variation, therefore making the recognition of subspecies untenable, these data need to be reexamined because they may have included specimens of its sibling species *A. chrysophilus* (Bronner et al. 2003; Chimimba and Bennett 2005). A comprehensive analysis of geographic variation involving a range of systematic techniques and a wide geographic coverage in Africa is needed.

DIAGNOSIS

Aethomys ineptus (Fig. 1) is externally indistinguishable from its sibling species, *A. chrysophilus* (Linzey and Chimimba 2008). It is a medium-sized, murid rodent (total length about 300 mm; head and body length 117–180 mm) with a long, sparsely haired tail (about 120% of head and body; 102.7–123.5%); skull < 41 mm in greatest length (32.4–40.5 mm) and relatively narrow (zygomatic width < 51% of greatest length; breadth of braincase 13.2–16.4 mm, greatest height of skull 10.4–12.3 mm); narrow molars (width of M1 about 2.0 mm; 1.62–2.00 mm); and strongly opisthodont incisors (Chimimba 1998; Chimimba et al. 1999; Linzey et al., in press a). Positive identification of *A. ineptus* requires examination of spermatozoa, the heads of which are spatulate (*A. chrysophilus* has a falciform-shaped sperm head—Breed et al. 1988; Visser and Robinson 1987); determination of diploid chromosome number ($2n = 44$ in *A. ineptus*, $2n = 50$ in *A. chrysophilus*—Gordon and Rautenbach 1980); allozyme analysis (hemoglobin of *A. ineptus* with either “fast” or “slow” bands, *A. chrysophilus* with only “slow” bands—G. Campbell, in litt.); or analysis of mitochondrial DNA (mtDNA—Linzey et al. 2003; Russo et al. 2006). Cranial morphometric analysis of positively identified specimens ($2n = 44$, $n = 4$; $2n = 50$, $n = 15$), augmented by specimens from the same localities ($2n = 44$, $n = 34$; $2n = 50$, $n = 6$), revealed the following diagnostic characters for the $2n = 44$ cytotype (*A. ineptus*) relative to the $2n = 50$ cytotype (*A. chrysophilus*): alisphenoid process of squamosal significantly narrower, and ratio of greatest cross-sectional crown width of M2 to greatest length of frontals averages 16.2% versus 17.4% and ratio of greatest cross-sectional crown width of m2 to greatest length of frontals 15.0% versus 16.3% (Chimimba 1998; Chimimba et al. 1999). However, species assignments of museum specimens based on these characters result in geographic distributions that are contradicted by those based on a larger number of positively identified specimens from an array of localities (Linzey et al. 2003) and need to be reexamined.

The only other coexisting species likely to be confused with *A. ineptus* is *Micaelamys namaquensis* (formerly

Aethomys namaquensis; see Musser and Carleton [2005]), which has a longer tail (about 135% of head and body), smaller skull (greatest length of skull < 35 mm; observed range 27.08–34.91 mm), and m1 with 3 cusps in anterior row (the m1 of *A. ineptus* has 2 cusps, often with a small additional tubercle or cingulum—Kesner et al., in press). Other *Aethomys* species currently known to occur outside the geographic range of *A. ineptus* are much larger (*A. silindensis*, skull length ≤ 43 mm) or have shorter tails (*A. nyikae*, 95–115% of head and body), wider molars (*A. nyikae*, M1 2.0–2.2 mm; *A. kaiseri*, M1 > 2.3 mm), wider skulls (*A. nyikae* and *A. kaiseri*, zygomatic width > 51% of skull length), and orthodont incisors (*A. nyikae* and *A. kaiseri*—Chimimba et al., in press; Linzey et al., in press b, in press c; Meester and Setzer 1971).

GENERAL CHARACTERS

General pelage coloration is similar to that of *A. chrysophilus* (Linzey and Chimimba 2008): dorsally reddish brown mixed with black or brownish black hairs, with a tendency for specimens from dry areas to be paler; pelage variously described as brown, orange-yellow, or cinnamon, depending on concentration of dark hairs; ventral hairs white or white with gray base; sharply demarcated dorsal and ventral coloration; soles of feet dusky, with upper surface covered with white or pale yellow-orange hairs; robust skull, with deep heavy rostrum; well-developed supraorbital and occipital ridges; broad palate; relatively large bullae (Fig. 2); molars heavy and angular, with prominent cusps; and a slight interorbital constriction.

Body measurements (in mm) of positively identified specimens from within the geographic range of *A. ineptus* (KwaZulu-Natal Province, South Africa) in the Transvaal Museum, Pretoria, South Africa (Linzey et al., in press a) are: total length, 309 (284–325), $n = 4$; length of tail, 162 (144–170), $n = 4$; length of hind foot, 30 (26–32), $n = 4$; and length of ear from notch, 20 (18–22), $n = 4$. Body mass (in g) and skull measurements (in mm) of positively identified specimens from Gauteng Province, South Africa, in the Transvaal Museum (Linzey et al., in press a) are: body mass, 82 (65–107), $n = 15$; greatest length of skull, 35.0 (33.0–37.1), $n = 15$; greatest width of skull, 14.3 (13.7–14.3), $n = 15$; and M1–M3, 5.8 (5.5–6.3), $n = 15$. An analysis of skull dimensions of specimens of *A. ineptus* from localities that (based on geographic distribution) included an approximately equal number of *A. ineptus* and *A. chrysophilus* revealed a general lack of sexual dimorphism (Chimimba and Dippenaar 1994).

DISTRIBUTION

The distributional range of *A. chrysophilus* (sensu lato) extends over a large area of sub-Saharan Africa (Chimimba



Fig. 2.—Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Aethomys ineptus* collected 14 miles northwest of Barberton, Limpopo Province, South Africa, on 23 November 1975 by L. Robbins (Carnegie Museum of Natural History, CMNH 41581). Greatest length of skull is 35.5 mm.

and Bennett 2005; De Graaff 1981; Musser and Carleton 1993, 2005; Skinner and Smithers 1990). Within this distributional range, however, positively identified specimens of *A. ineptus* ($n = 127$ from 27 localities in South Africa and 1 locality in Swaziland) suggest that its distribution is much narrower than that of its sibling species, *A. chrysophilus* (Fig. 3; Linzey et al. 2003, in press a; I. Russo, in litt.). In South Africa, *A. ineptus* is the exclusive occupant of areas of higher elevation in the interior, and the area south of approximately 25°S, reaching its southern limit slightly south of Durban, KwaZulu-Natal Province (30°03'S—Linzey et al. 2003). Although the species may

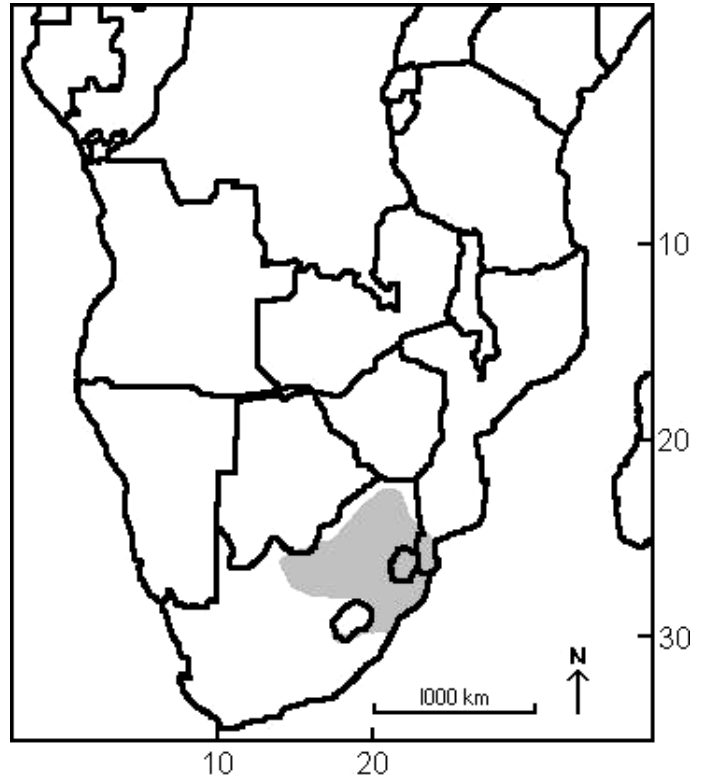


Fig. 3.—Geographic distribution of *Aethomys ineptus* in Africa (modified from Linzey et al., in press a).

occur in adjoining areas of Mozambique and Botswana, there are no positively identified specimens from Mozambique and the only positively identified individual from Botswana is *A. chrysophilus* (Linzey and Chimimba 2008). A specimen with a chromosome number of $2n = 44$ was reported from the Ivory Coast (Matthey 1958), but it has been established that this specimen originated from South Africa (Chimimba 1998).

The precise distributional limits of *A. ineptus* are incompletely known. In eastern South Africa, the geographic ranges of the 2 sibling species appear to meet in Kruger National Park between the Olifants River (24°01'S for *A. chrysophilus*) and the area surrounding Satara Camp (24°21'S for *A. ineptus*), a distance of 40 km (Linzey et al. 2003). The species have been collected within 35 km of each other at Tzaneen, Limpopo Province (30°10'E for *A. ineptus*), and Letsitele (30°18'E for *A. chrysophilus*—Linzey et al. 2003). In the west, there is an area of distributional overlap in North West and Gauteng provinces (Magaliesberg region), and in northern Limpopo Province southeast of Alldays (Langjan Nature Reserve—Linzey et al. 2003). The latter is approximately 40 km northwest of localities with the same or higher elevations that only harbor *A. ineptus* (Linzey et al. 2003). Further west and southwest, only *A. ineptus* has been recorded from 25°35'S southward (Botsalano Game Reserve, Kuruman, Reivilo—Linzey et al. 2003).

Records for positively identified individuals indicate that the distributional ranges of *A. ineptus* and its sibling species, *A. chrysophilus*, are largely parapatric (Linzey et al. 2003). Although syntopy is likely in the zone of parapatry, based on mtDNA data only 1 locality is known to harbor both species (Langjan Nature Reserve, near Alldays, northern Limpopo Province, South Africa—Linzey et al. 2003). Despite both species having been reported to occur in Pilanesburg National Park, North West Province, South Africa, local sympatry cannot be verified because the exact sites of collection are unknown (Linzey et al. 2003).

FOSSIL RECORD

Although there is an approximately 3.7-million-year-old fossil of *A. chrysophilus* (sensu lato) from Makapansgat, Limpopo Province, South Africa (Pocock 1987), there is no specific fossil record for *A. ineptus*.

FORM AND FUNCTION

Dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16. *A. ineptus* has multicusped molars that are generally primitive in structure and, as proposed for *A. chrysophilus*, this molar morphology suggests an omnivorous diet (Denys 1994). *A. chrysophilus* (sensu lato) has a morphologically primitive stomach (unilocular–hemiglandular) and a large cecum, but lacks a gall bladder, characteristics that suggest an adaptation for herbivory (Perrin and Curtis 1980).

Spermatozoa of *A. ineptus* differ from those of all other murid rodents thus far examined in having a spatulate-shaped head. The head is about 4.3–6 μm in length, midpiece about 15–18 μm in length, and the principal plus end piece is about 43–57 μm . Under fluorescence and transmission electron microscopy, the mature sperm head is seen to exhibit relatively uncondensed chromatin and a large acrosome that is caudally flexed so that it lies along 1 side of the head (Breed 1995, 1997; Breed et al. 1988; Gordon and Watson 1986; Visser and Robinson 1987). In addition, *A. ineptus* exhibits a large percentage of grossly abnormal, relatively small sperm, and small testes relative to body mass, characteristics that suggest minimal intermale sperm competition within the female reproductive tract (Breed 1995; Breed and Taylor 2000). The baculum of *A. ineptus*, like that of *A. chrysophilus*, exhibits a gradual transition between the shaft and base (Visser and Robinson 1987).

The brain of *A. ineptus* is heavy relative to its body weight and, among South African species studied, only exceeded by *Tatera leucogaster* and *Elephantulus brachyrhynchus* (Monadjem 1998). Mean brain weight and dimensions ($n = 5$) are: weight 0.822 g, length 19.1 mm, height 6.7 mm, width 10.4 mm, and hemisphere length 10.4 mm.

ONTOGENY AND REPRODUCTION

In north-central South Africa, *A. ineptus* is a seasonal breeder, with reproduction confined predominantly to the Southern Hemisphere summer (December–February) and autumn months (March–May—Muteka et al. 2006b). In males, seminiferous tubule diameters are significantly larger between September and February relative to between March and August and, although spermatogenesis is prevalent in winter (June–August), the number of spermatozoa in the epididymides decreases in spring (September–November), summer (December–February), and autumn (March–May). Testicular mass relative to body mass and testicular volume regresses between May and September but shows recrudescence between September and April, whereas plasma testosterone concentrations increase significantly between September and February relative to between March and August. In females, corpora lutea are present throughout the year, but decrease in number during winter, whereas mean plasma progesterone concentration increases significantly between August and November and again between February and April. This bimodal pattern of progesterone concentration suggests that there may be up to 2 litters per breeding season. Gravid females are found between October and April, whereas gravid or lactating females are conspicuously absent between May and September. However, presence of follicular development in females and occurrence of corpora lutea outside the breeding season imply that *A. ineptus* may undergo spontaneous ovulation. Mean litter size in KwaZulu-Natal, South Africa, is 2.7 (range = 1–3, $n = 6$ —Taylor 1998).

A comparison of male *A. ineptus* maintained under short (8L:16D) and long (16L:8D) photoperiods suggests that this species is photoperiodically responsive to long days (Muteka et al. 2006a). After 3 months of exposure, individuals exposed to the long-day treatment showed significantly higher testicular mass relative to body mass, greater testicular volume, and larger seminiferous tubule diameters. However, plasma testosterone concentrations were not significantly different between the 2 photoperiodic treatments.

ECOLOGY

Population characteristics.—*Aethomys ineptus* generally occurs in low to moderate densities. Typically, density is < 18 individuals/ha (Ferreira and van Aarde 1999; Miller 1994; Monadjem and Perrin 1998), although 1 of us (A. Linzey) and a collaborator have recorded numbers as high as 37 individuals/ha near Pietermaritzburg, KwaZulu-Natal Province, South Africa. In South Africa, Kern (1981) reported on annual variation in population density that ranged from 1.01 individuals/ha in January (summer) to 3.24 individuals/ha in July (winter dry season). Year-to-year variation was exhibited at Vaalkop Dam Nature Reserve,

North West Province, South Africa, where *A. ineptus* comprised 6.7% and 46.5% of the small mammal community (14 species) in different years (Ellison 1990). Because the species requires substantial cover, drought, overgrazing, and fire can negatively affect population densities (Bowland 1986; Bowland and Perrin 1988, 1989).

Space use.—Very little is known about the ecology of *A. ineptus*. Like its sibling species, *A. chrysophilus*, the Tete veld rat prefers habitats where there is substantial cover in the form of shrubs, rocks, and herbaceous vegetation (Avenant and Kuyler 2003; Ferreira and van Aarde 1999; Linzey et al. 2003; Monadjem 1997a). However, within such habitats, *A. ineptus* is found at a wider range of elevations and climatic conditions than *A. chrysophilus*. In north-central South Africa, the major portion of the species' distributional range is > 1,000 m in elevation, but it occurs as low as 800 m on the western side of the Soutpansberg Range (Linzey et al. 2003). In Swaziland, Tete veld rats have been collected at elevations ranging from 160 to 1,450 m (Monadjem 1999) and the species inhabits coastal dune forests north of Durban (KwaZulu-Natal Province, South Africa—Ferreira and van Aarde 1999).

Diet.—The Tete veld rat is considered to be omnivorous, with its diet composed approximately of 38–59% vegetation, 34–58% seeds, and 0–9% insects (Miller 1994; Monadjem 1997b). In Kruger National Park, South Africa, Kern (1981) recorded a home range between 1,500 and 3,000 m².

Diseases and parasites.—Parasites reported from *A. ineptus* in southern Kruger National Park, Mpumalanga Province, South Africa, include the flea *Xenopsylla brasiliensis*, louse *Hoplopleura petersoni*, and ticks *Haemaphysalis leachii spinulosa* and *Rhipicephalus simus* (Braack et al. 1996). Although mostly identified to the genus level, 13 species of mites in 6 families and 3 suborders (suborder Mesostigmata: Laelapidae—*Androlaelaps*, *Laelaps vansomereni*, *Laelaps*; suborder Prostigmata: Trombiculidae—*Gahrlipeia* (G.), *Guntherana* (?), *Odontacarus*, *Schoutedeniichia* (?); suborder Astigmata: Myocoptidae—*Myocptes*, *Trichoecius*; Listrophoridae—*Afro-listrophorus* (?); Atopomolidae—*Listrophoroides*, (*Olistrophoroides*) (?); Glycyphagidae), some of which may represent a number of new mite species, have also been reported from *A. ineptus* (Braack et al. 1996). Gaboon adders (*Bitis gabonica gabonica*) studied in KwaZulu-Natal Province, South Africa, included Tete veld rats in their diet (Perrin and Bodbijn 2001).

Interspecific interactions.—Small mammal associates of *A. ineptus* include many of the same species that coexist with its sibling species, *A. chrysophilus* (Linzey and Chimimba 2008). In coastal dune forests of KwaZulu-Natal Province, South Africa, they co-occur with *Saccostomus campestris* and *Mastomys natalensis* (Ferreira and van Aarde 1999). At Vaalkop Dam Nature Reserve, North West Province, South Africa, *A. ineptus* was found with *Suncus lixus*, *Crociodura hirta*, *C. cyanea*, *Elephantulus brachyrhynchus*, *Graphiurus murinus*, *Tatera leucogaster*, *Steatomys pratensis*, *S. campestris*, *Otomys irroratus*, *Lemmiscomys rosalia*, *Mus minutoides*, *M. natalensis*, and *Rhabdomys pumilio* (Ellison 1990). In a

survey of 39 localities across Swaziland, *A. ineptus* co-occurred with as many as 14 other small mammal species, although communities with 3 or 4 other species were most common. Most frequent associates were *M. natalensis*, *L. rosalia*, and *M. minutoides* (Monadjem 1999).

Miscellaneous.—Tete veld rats have been maintained and successfully bred in captivity (Muteka et al. 2006a).

BEHAVIOR

Aethomys ineptus is nocturnal, with greater activity early in the night (Perrin 1981). The species also is categorized as semiarboreal by Monadjem (1998), who correlated this behavior and nocturnality with its relatively large brain size. Based on reproductive characteristics that suggest minimal intermale sperm competition within the female reproductive tract, Breed (1995) hypothesized that *A. ineptus* is (or was in the past) likely to be monogamous.

GENETICS

Cytogenetics.—Diploid chromosome number in *A. ineptus* is $2n = 44$, in contrast with $2n = 50$ in its sibling species, *A. chrysophilus*. No individuals with intermediate diploid numbers have been collected and no interbreeding has been reported to occur in captivity. The pronounced difference in sperm morphology of the 2 species likely constitutes a prezygotic isolating mechanism (Gordon and Rautenbach 1980; Visser and Robinson 1987).

G-banded karyotyping of *A. ineptus* revealed 3 groups of autosomes that differed in size and position of centromeres (Visser and Robinson 1986). There are 8 pairs of metacentric chromosomes (3 large and 5 small) and 13 pairs of acrocentric chromosomes. The sex chromosomes consist of a large acrocentric X and a smaller submetacentric Y chromosome (Baker et al. 1988; Visser and Robinson 1987). Banding patterns of all but 2 chromosomes could be matched in the karyotypes of the 2 species, with chromosome 4 in *A. ineptus* and chromosome 20 in *A. chrysophilus* remaining after all others had been matched. G-band patterns of both sex chromosomes also differed between species (Visser and Robinson 1987). It is thought that the $2n = 44$ cytotype in *A. ineptus* is derived from 3 fusion products that correspond to the unfused acrocentric elements 1/2, 3/4, and 5/8 present in the $2n = 50$ cytotype, and that the $2n = 50$ cytotype represents the primitive condition (Visser and Robinson 1987).

Molecular genetics.—The hemoglobin electromorph of *A. ineptus* has been described as producing a “fast” double band in comparison with a “slow” double band in *A. chrysophilus* (Gordon and Watson 1986). Allozyme studies of a larger number of individuals from a wider array of localities subsequently revealed that hemoglobin of *A. ineptus* is polymorphic (G. Campbell, in litt.).

A molecular study of *A. ineptus* and *A. chrysophilus* from southern Africa was recently undertaken by Russo et al. (2006). Phylogenetic and phylogeographic analyses of mtDNA sequences showed reciprocal monophyly between 2 populations of the 2 sibling species in southern Africa, but no support for monophyly of *A. chrysophilus* from southern and eastern Africa. This suggests that analysis of mtDNA can be used to distinguish these 2 sister species in southern Africa. However, Russo et al. (2006) suggest that these results need to be investigated further by DNA analyses of type specimens and topotypical material.

CONSERVATION

The International Union for Conservation of Nature and Natural Resources (2007) lists the status of *A. ineptus* as a “least concern” species.

REMARKS

Except as noted, data included in this account are derived only from areas reasonably certain to be within the distributional range of *A. ineptus* (and not *A. chrysophilus*). Hence, we have not used information from Botswana, Namibia, southern Mozambique, or from the zone of parapatry in South Africa. The genus name is derived from Greek, with *Aethomys* being a combination of *aithos* (= sunburned) and *mys* (= mouse), whereas the species name is probably derived from the Latin word *ineptus* meaning unsuitable, out of place, tasteless, or silly. This suggests that Thomas and Wroughton (1908) may have considered the paler color not to conform and therefore “unsuitable” for a typical “golden”-colored *A. chrysophilus* (Chimimba 1998). Chimimba (1998) proposed the common English name Tete veld rat after Tete, the type locality.

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