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Petrodromus tetradactylus.

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Petrodromus Peters, 1846

Petrodromus Peters, 1846:257. Type species *Petrodromus tetradactylus* Peters.
Cercoctenus Hollister, 1916:1. Type species *Petrodromus sultan* Thomas.
Mesoctenus Thomas, 1918:366. Type species *Petrodromus rovumae* Thomas.

CONTEXT AND CONTENT. Superorder Afrotheria (Springer et al. 1999), order Macroscelidea (Butler 1956), family Macroscelididae, subfamily Macroscelidinae. *Petrodromus* is monotypic (Corbet 1974; Corbet and Hanks 1968).

Petrodromus tetradactylus Peters, 1846

Four-toed Elephant-shrew

Petrodromus tetradactylus Peters, 1846:258. Type locality "Tette, Mozambique."
Petrodromus rovumae Thomas, 1897:434. Type locality "Rovuma River, 100 miles (= 161 km) inland" (on Tanzania side of river, vide Corbet and Hanks 1968).
Petrodromus sultani Thomas, 1897:435. Type locality "Mombassa [= Mombasa], Kenya" (corrected to *sultan* by Thomas 1898).
Petrodromus matshiei Neumann, 1900:540. Type locality "Burunge" (= Barungi, Tanzania).
Petrodromus nigriseta Neumann, 1900:541. Nomen nudum.
Petrodromus venustus Thomas, 1903:339. Type locality "Namwiwe, Zambia."
Petrodromus tordayi Thomas, 1910:84. Type locality "Misumba, Sankuru River, Congo" (= Democratic Republic of Congo).
Petrodromus occidentalis Roberts, 1913:69. Type locality "n(orth)w(estern) Rhodesia" (= Zimbabwe).
Petrodromus robustus Thomas, 1918:367. Type locality "upper Lufira River, alt. about 3,600 ft (= 1,097 m), Katanga, Congo" (= Democratic Republic of the Congo).
Petrodromus mossambicus Thomas, 1918:369. Type locality "Cabaceira in Mozambique."

CONTEXT AND CONTENT. Context as for genus. Ten subspecies are recognized (Corbet and Hanks 1968):

P. t. beirae Roberts, 1913:69. Type locality "Zimbiti, Beira, Mozambique."
P. t. rovumae Thomas, 1897:434, see above (*mossambicus* Thomas and *nigriseta* Neumann are synonyms).
P. t. sangi Heller, 1912:12. Type locality "summit of Mount Mbololo, alt. 4,000 ft (= 1,219 m), Taiti (= Taita) Hills," Kenya.
P. t. schwanni Thomas and Wroughton, 1907:289. Type locality "Coguno, Inhambane," Mozambique.
P. t. sultani Thomas, 1897:435, see above.
P. t. swynnertoni Thomas, 1918:368. Type locality "Chirinda Forest, alt. 3,900 ft (= 1,189 m), Melsetter, Rhodesia" (= Zimbabwe).
P. t. tetradactylus Peters, 1846:257, see above (*matschiei* Neumann, *occidentalis* Roberts, *robustus* Thomas, and *venustus* Thomas are synonyms).
P. t. tordayi Thomas, 1910:84. Type locality "Misumba, Sankuru River, Congo" (= Democratic Republic of the Congo; *tumbanus* Kershaw is a synonym).
P. t. warreni Thomas, 1918:364. Type locality "Mangazi, Zululand (= KwaZulu-Natal)," South Africa.
P. t. zanzibaricus Corbet and Neal, 1965:68. Type locality "Makunduchi, Zanzibar Island."

DIAGNOSIS. Four-toed elephant-shrews (Fig. 1) are distinguishable from all other Macroscelidinae by absence of a hallux and presence of 2 pairs of antebrachial and pectoral mammae (Corbet and Hanks 1968). The light and dark facial pattern surrounding eye is shared only with *Elephantulus rufescens* (Corbet and Hanks 1968).

Petrodromus tetradactylus is the most primitive member of the family (Evans 1942), with proportionally the narrowest skull, smallest olfactory chamber, most constricted interorbital region, and smallest brain case and bullae. Compared with other elephant-shrews, forelegs are proportionally longer than rear legs, and elements of forelegs are proportionally longer than corresponding parts in other genera (Evans 1942).

GENERAL CHARACTERS. The 4-toed elephant-shrew is a large (total length ≤ 375 mm) macroscelidean that is characterized by an elongated, trunk-like snout; broad, upstanding ears; large eyes; short fore limbs; long hind limbs; soft fur; a naked patch of skin at base of the tail; and a long, slender tail sparsely covered with hair or bristles on the ventrum.

Dorsal color varies from rusty red, buffy-gray, to dark brown with buff- or orange-colored flanks (Skinner and Smithers 1990). A wide dorsal stripe is present in some subspecies, but indistinct or absent in the others (Corbet and Neal 1965). Undersides are white (Corbet and Hanks 1968), but in female *P. t. sangi* underparts are washed with ochraceous-buff (Hollister 1918). *P. t. sultan* males have a white band across the throat that females lack, and females have a pink wash in inguinal area compared with a yellow wash in males (Corbet and Neal 1965). Four-toed elephant-shrews have a band of white fur along upper lip and a conspicuous white ring around eye that is interrupted posteriorly by an irregular dark brown to black spot that extends back to below ear. Ears are rusty-brown, with pure white hair on base of the inner margin (Skinner and Smithers 1990). Upper parts of feet are buffy-yellow. Tail is blackish on upper side and buffy on under side, but darkening in middle and almost black at tip (Skinner and Smithers 1990).

Range of adult body mass is 160–280 g (FitzGibbon 1995; Skinner and Smithers 1990). In a fully mature adult, length of head and body is ca. 165–205 mm and length of tail is ca. 160–170 mm (Smithers and Wilson 1979). Average measurements (in mm, range in parentheses) of 10 male and 10 female *P. tetradactylus* from Zimbabwe (Smithers and Wilson 1979) are, respectively: total length, 350 (324–370), 355 (337–373); length of tail, 162 (160–

FIG. 1. Adult 4-toed elephant-shrew, *Petrodromus tetradactylus*, from Msabaha, Kilifi District, Coast Province, Kenya. Photograph by G. B. Rathbun.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult male *Petrodromus tetradactylus* from Changombe, Rabai, 39°34′E, 3°54′S, 183 m, Mombasa District, Coast Province, Kenya (California Academy of Sciences 24529). Greatest length of the skull is 56.9 mm.

176), 163 (162–170); length of hind foot, 59 (57–67), 58 (55–62); length of ear, 35 (33–37), 35 (32–37).

Skull (Fig. 2) is relatively long (condylobasal length >45 mm), and length of upper tooth row is >25 mm. Zygomatic arches are complete and jugals are large. Auditory bullae have prominent ectotympanic, entotympanic, and sphenoidal elements. Lachrymals are very large. Sagittal crest is restricted to posterior half of the pariatals. Palate is relatively entire and lacks large perforations between first molars. Maxillary I1 is nearly twice as long as I2 and I3; I3 is double-rooted (Corbet and Hanks 1968).

Petrodromus tetradactylus females may be larger than males (Corbet and Neal 1965). In Zimbabwe, females are larger than males (Skinner and Smithers 1990), but average head and body length for 10 females (192 mm) is only 4 mm larger than for 10 males, and body masses associated with the specimens are irreconcilably inconsistent (Skinner and Smithers 1990; Smithers and Wilson 1979). Mean (±*SD*) length of head and body for 16 males (196.2 ± 9.7 mm) and 16 females (195.3 ± 6.5 mm) from coastal Kilifi District, Kenya, is not statistically different (G. B. Rathbun, in litt.). Mean (±*SE*) mass of 14 males (198 ± 6 g) and 6 females (208 ± 11 g) also from Kilifi District (FitzGibbon 1995) as well as mean (±*SD*) length of head and body for 15 males (190.6 ± 20.3 mm) and 9 females (200.0 ± 10.0 mm) inland from Mombasa, Kenya, do not differ statistically (Hollister 1918). In more inland or southern areas of the distribution, females may be slightly larger than males.

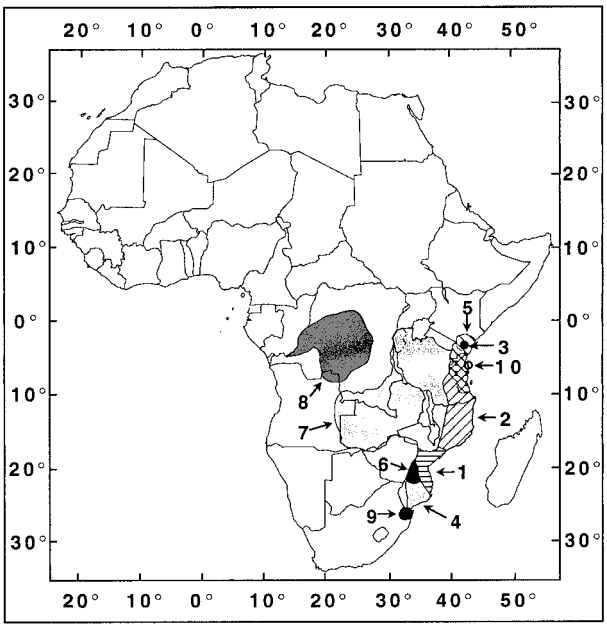

FIG. 3. Distribution of *Petrodromus tetradactylus* in central, eastern, and southern Africa. Subspecies are: (1) *P. t. beirae*; (2) *P. t. rovumae*; (3) *P. t. sangi*; (4) *P. t. schwanni*; (5) *P. t. sultan*; (6) *P. t. swynnertoni*; (7) *P. t. tetradactylus*; (8) *P. t. tordayi*; (9) *P. t. warreni*; (10) *P. t. zanzibaricus*. Crosshatched area is zone of intergradation between *P. t. sultan* and *P. t. rovumae*.

DISTRIBUTION. *Petrodromus tetradactylus* is restricted to Africa (Fig. 3). It occurs in central and southeastern regions where rainfall exceeds about 700 mm/year, and woody vegetation provides suitable cover (Corbet and Hanks 1968; Nicoll and Rathbun 1990; Smithers 1986). The 4-toed elephant-shrew is the 2nd most widespread species (following *Elephantulus brachyrhynchus*). It occurs in Angola, Democratic Republic of the Congo, Kenya, Mozambique, Malawi, South Africa, Sudan, Tanzania, Uganda, Zambia, and Zimbabwe (Nicoll and Rathbun 1990). Elevational range is from sea level to ca. 1,400 m in Taita Hills, Kenya (Heller 1912).

Petrodromus tetradactylus sultan of coastal eastern Africa may have been more widespread and separated by arid habitats from the inland *P. t. tordayi*. These 2 forms subsequently interbred when *P. t. tordayi* invaded coastal areas. This may have created the string of subspecies along the coast, south of *P. t. sultan* (Corbet and Neal 1965). *P. t. zanzibaricus* may have been introduced to Zanzibar Island (Corbet and Neal 1965), but R. H. W. Pakenham (in litt.) argues against this based on ethnology of the local people. The isolated distribution of *P. t. tordayi* south of the River Congo in central Africa may be indicative of a relict population that first occupied this region 10,000–40,000 years ago when it was more arid, and as conditions became wetter the 4-toed elephant-shrew became secondarily adapted to the current forest conditions (Kingdon 1971).

FOSSIL RECORD. *Petrodromus tetradactylus* is only known from the middle to late Pleistocene of Africa, which is the briefest fossil record of the 4 extant genera (Butler 1995).

FORM AND FUNCTION. Color of pelage varies geographically and can distinguish subspecies (Corbet and Neal 1965). Bristles along bottom of tail are 1–7-mm long (Corbet and Hanks 1965; Thomas 1918, 1919). Shape of the bristles varies geographically from no expanded distal ends, through a club shaped end, to a knobbed tip. These unique bristles may result from singeing during wild fires (Roberts 1913; Thomas 1918) or may function in detection of ground vibrations (Corbet and Neal 1965) or in scent marking (Rathbun 1976). The large multilobulate, alveolar, sebaceous, and tubular sweat glands at the base of each clubbed bristle in animals from Kenya suggest that the bristles aid in scent marking (Sokolov et al. 1980).

Dental formula is i 3/3, c 1/1, p 4/4, m 2/2, total 40 (Evans

1942). Vertebral formula is 7 C, 13 T, 7 L, 3 S, 25–28 Ca, total 55–58 (de Balsac and Bourlière 1955).

Jaw musculature of *P. tetradactylus* is unique (Coldiron 1977). M. masseter and pars reflexa are restricted to lateral surface of jaw, tendon sheet covers dorsal half of M. zygomaticomandibularis, M. pterygoideus internus origin is on palatine in orbital wall, and M. digastricus originates from mastoid process and inserts under ascending ramus.

The 4-toed elephant-shrew has abdominal testes, a long epididymis that stores sperm, and an extremely long penis with the corpus cavernosum making up most of the erectile tissue (Woodall 1995a). The tip of glans penis is spear-shaped with 2 lateral lobes (Woodall 1995b).

Spermatozoa are ca. 79 μm long with a broad, pointed, spatulate head and narrow (0.85 μm) midpiece (Woodall 1991). Nucleus (longitudinal section) is wedge-shaped, wider distally, with a proximal groove. Acrosome is bulbous, and subacrosome is flat-topped and prominent. Mitochondria have 37 gyres (Woodall 1991).

Petrodromus tetradactylus has a short large intestine (8.6% of 13.9 cm, compared to ca. 16–21% for other elephant-shrew species), the presence of which may be related to less severe water conservation requirements in the more mesic habitats it occupies (Woodall 1987). The kidney of *P. tetradactylus* has distinct cortical and medullary zones, and a single elongated urinary papilla projects into the pelvis with no calices (Downs 1996). The average (±*SE*) urine osmolality on a water-free diet for *P. tetradactylus* was 2.96 ± 0.19 mol/kg (Downs 1996).

The 4-toed elephant-shrew is able to maintain a relatively stable body temperature (33.1–37.5°C) through a wide range of ambient temperatures, and it has a thermal neutral zone of 25–34°C. Its basal metabolic rate (±*SE*) is 0.871 ± 0.027 ml O_2 g^{-1} h^{-1}. Maximum heat loss through evaporative cooling at 38°C is 32.6% (Downs and Perrin 1995).

ONTOGENY AND REPRODUCTION. *Petrodromus tetradactylus* is oligo-ovulating (Tripp 1971). Although female 4-toed elephant-shrews typically carry single embryos and produce single young (Brown 1964; Rathbun 1979; Tripp 1971), 2 embryos occurred in 1 of 2 females from Zambia (Sheppe 1973) and in 2 of 3 females from Zimbabwe (Smithers and Wilson 1979).

Neonatal *P. tetradactylus* are highly precocial; they are fully furred with adult color, their eyes are open, and they are able to walk within hours (Ansell 1963; Tripp 1972). Birth weight is ca. 31.5 g, with a daily gain of ca. 2 g (Tripp 1972). *P. tetradactylus* has been maintained in captivity (Ansell and Ansell 1969; Rathbun 1979; Tripp 1972), but it has not conceived in captivity (Nicoll and Rathbun 1990). Females captured in late pregnancy are prone to abort (Kingdon 1974; G. B. Rathbun, in litt.), although successful parturition may occur (Tripp 1972).

In southern Africa breeding occurs during the wet months of August through October (Skinner and Smithers 1990). Pooling data from throughout its distribution, pregnant females were found in all months except March, May, September, and November (Brown 1964; G. B. Rathbun, in litt.; Sheppe 1973; Smithers and Wilson 1979). Seasonality of reproduction may increase from tropical to temperate regions.

ECOLOGY. Four-toed elephant-shrews are physiologically adapted to mesic regions (Perrin 1995), where they occur in scrub, woodland, and forest habitats with dense woody undergrowth and associated thickets. In the more arid regions of Africa, these habitats are often associated with rocky outcrops, riparian zones, or coastal areas. Because of the vegetative cover in these habitats, the substrate is often covered with a layer of leaf litter, and *P. tetradactylus* often builds and uses a network of runs through this dense material.

Ants and termites are particularly important prey in many areas of Africa, but some green plant matter, fruits, and seeds are also eaten (Ansell and Ansell 1969; FitzGibbon 1995; Loveridge 1922; Sheppe 1973; Skinner and Smithers 1990). In coastal Kenya, their diet (in decreasing order of percent importance) includes beetles (22.5%), termites (4.7%), plant matter (4.6%), centipedes (3.1%), ants (2.9%), crickets and cockroaches (1.6%), and millipedes, spiders, and others (<1.0%—Rathbun 1976).

In areas of the Arabuko-Sokoke Forest of coastal Kenya that are dominated by *Afzalia* trees, *P. tetradactylus* attains densities of 2.1 individuals/ha. However, in parts of the forest dominated by *Cynometra* trees densities can be about twice as high, and about half as high in areas dominated by *Brachystegia* trees. These differences may be related to the availability of invertebrate prey and the preference for low cover in dense thickets (FitzGibbon 1995). In the Arabuko-Sokoke Forest, radio-collared *P. tetradactylus* occupy home ranges that are 1.2 ± 0.2 ha (n = 14), with no difference between the sexes and a high degree of overlap between males and females (FitzGibbon 1995).

The diurnal golden-rumped elephant-shrew (*Rhynchocyon chrysopygus*) is sometimes sympatric and syntopic with *P. tetradactylus* in coastal forests of northern Kenya. However, the 2 species avoid competition because the latter has a smaller body size and preys on slightly different invertebrates, prefers microhabitats with denser cover, and is crepuscular (FitzGibbon 1995).

Four-toed elephant-shrews face the same predators as other small mammals, including snakes such as the Gaboon viper (*Bitis gabonica*—Bruorton 1992), raptors, and carnivores. Domestic cats (*Felis catus*) are also likely predators (Ansell and Ansell 1969).

Petrodromus tetradactylus is host to over a dozen *Ixodes* and *Rhipicephalus* tick species, which often concentrate at base and margin of ears and near base of tail (Ansell and Ansell 1969; Fourie et al. 1995; Loveridge 1922; Rathbun 1976). Heavy infestations of mites, tentatively identified as *Androlaelaps, Euschoengastia,* and *Schoengastia* often occur at base of ears and tail (Fourie et al. 1995; Rathbun 1976). Several species of fleas, including *Chimaeropsylla haddowi, Chimaeropsylla potis, Ctenocephalides felis,* and *Echidnophaga gallinacea* have been recorded from *P. tetradactylus* (Fourie et al. 1995). No fleas were found on specimens from coastal Kenya (Rathbun 1976). The 4-toed elephant-shrew is also host to the sucking louse *Neolinognathus elephantuli* (Fourie et al. 1995). Macroendoparasites include acanthocephalan larvae in the peritoneum, and species of *Cloeascaris, Subulura,* and *Travasospirura* gastrointestinal worms (Rathbun 1976). Blood parasites include *Plasmodium brodeni, Trypanosoma petrodromi,* and spirurid (filarial) worms (Bruce 1915; Hoogstrall et al. 1950; Keymer 1971).

In the Arabuko-Sokoke Forest, the Giriama people trap *P. tetradactylus* for meat using snares and deadfalls. Despite the yearly removal of an estimated 15 individuals/km^2, the harvest is probably sustainable (FitzGibbon et al. 1995).

Animals captured by snares that do not sustain physical injuries often die later of stress (Brown 1964). Better survival can be achieved by placing unbaited live traps on their paths (Ansell and Ansell 1969; Tripp 1972) or by chasing animals into fine nets (FitzGibbon 1995; Loveridge 1922). Colored ear-tags (Rathbun 1979) and radio-collars (FitzGibbon 1995) have been successfully used to mark 4-toed elephant-shrews.

BEHAVIOR. *Petrodromus tetradactylus* is terrestrial, highly cursorial, and very alert (Rathbun 1984). It is mainly active at dawn and dusk, with lesser periods of activity during the night, and least during midday (FitzGibbon 1995; Rathbun 1979; Woodall et al. 1989).

In captivity, 4-toed elephant-shrews actively maintain their paths by sweeping matter aside with their forefeet (Rathbun 1979). Runs are typically composed of a series of bare patches (Ansell and Ansell 1969; Sheppe 1973) where they land while running along the trails as they travel between sheltering and feeding areas (Brown 1964). *P. tetradactylus* is not bipedal (Kingdon 1974) and its limb proportions are intermediate between those of ricochetal and quadrupedal rodents (Evans 1942). When running, it carries its tail upright.

Leaf litter near trails is sometimes disturbed by foraging activity (Brown 1964), which includes using hind feet to scuff debris and using the long mobile nose as a probe (Allen and Loveridge 1927; Kingdon 1974). The long extendible tongue is used in an anteater fashion to glean small invertebrates from the surface of debris (G. B. Rathbun, in litt.).

When pursued, 4-toed elephant-shrews take shelter in hollow tree trunks, under logs, and in holes in termitaria or in the ground (Ansell and Ansell 1969; Brown 1964). However, they do not use these refugia as nests (Brown 1964; Kingdon 1974), and in captivity they do not use nesting material (G. B. Rathbun, in litt.). Captive animals prefer to rest in the open, often on top of nest boxes or shelters. They are always very alert, and even while at favored resting sites they rarely, if ever, close their eyes or lie on their sides (Ansell and Ansell 1969; Rathbun 1979).

Petrodromus tetradactylus may be solitary (Ansell 1960) or facultatively monogamous (FitzGibbon 1995, 1997; Rathbun 1979). Based on observations in captivity, they are also probably territorial. When kept as male–female pairs they fight less then when housed in same-sexed pairs or larger groups (Rathbun 1979). Fighting behaviors include rising on their rear legs and "boxing" with their front feet as well as lunging at one another (Rathbun 1979).

Grooming behaviors include face-washing, scratching with rear feet, and sand-bathing (Rathbun 1979). Captive *P. tetradactylus* are docile, easily handled, and make no attempt to bite (Ansell and Ansell 1969). They habituate relatively easily to artificial diets (Ansell and Ansell 1969; Tripp 1972), such as chopped hard-boiled egg, whole milk, and a mixture of ground raw horse meat and fine bone meal moistened with cod-liver oil (Crandall 1965).

Four-toed elephant-shrews have a keen sense of sight, smell, and hearing, but vocalizations are not common or well developed. In captivity, they make soft "purring" and "clucking" sounds, and when captured they sometimes scream loudly (Ansell and Ansell 1969; Kingdon 1974; G. B. Rathbun, in litt.). When disturbed, captive and free-ranging animals frequently foot-drum loudly on the substrate with their rear feet (Ansell and Ansell 1969; Brown 1964; Rathbun 1979; Sheppe 1973; Tripp 1972), which may function in intraspecific communication (Kingdon 1974). Captive *P. tetradactylus* sometimes wipe the substrate with the bottom surface of their tails in a side-to-side motion that may be associated with scent marking (Rathbun 1976).

GENETICS. *Petrodromus tetradactylus* has a diploid number of 2n = 28 with 8 pairs of metacentric and submetacentric chromosomes, 5 pairs of subtelocentric and acrocentric chromosomes, and a small pair of subtelocentric autosomes (Tolliver et al. 1989; Wenhold and Robinson 1987).

CONSERVATION STATUS. The 4-toed elephant-shrew is not threatened. However, 2 subspecies have special conservation status. *P. tetradactylus sangi* in the Taita Hills of Kenya is seriously threatened (and may already be extinct) caused by its restricted distribution and loss of habitat (Nicoll and Rathbun 1990). In 1993 the IUCN (now called The World Conservation Union) listed this taxon as "Insufficiently Known" (Groombridge 1993). However, in a more recent update of the list, the Taita Hills endemic was not classified (Baillie and Groombridge 1996). *P. tetradactylus beirae* is listed as "rare" based on its restricted distribution in riparian forest and associated thickets in KwaZulu-Natal, South Africa, but the lack of specific threats reduce conservation concern. In addition, its distribution extends beyond South Africa (Smithers 1986).

REMARKS. *Petrodromus tetradactylus sultan* is the most morphologically distinct subspecies (Corbet and Neal 1965), but it apparently hybridizes with *P. t. rovumae* where the distributions overlap (Fig. 3). *P. tetradactylus tordayi* is not only morphologically distinct, but it is also the only geographically isolated subspecies, and thus "must be considered a potential species" (Corbet and Hanks 1968). Based on analyses of allozyme variation in several species of Macroscelidinae, *Petrodromus* and *Macroscelides* are more closely related to each other than to any representatives of *Elephantulus* (Raman and Perrin 1997; Tolliver et al. 1989).

Macroscelids traditionally have been considered a family in the order Insectivora, or in the order Menotyphla with tupaiids (Patterson 1965). More recently, elephant-shrews have been associated with extinct Asian anagalids and lagomorphs based on foot morphology (McKenna 1975), but this association has not been supported by other morphological comparisons, including jaw musculature (Coldiron 1977) and male reproductive system (Woodall 1991, 1995a, 1995b). Currently, based on morphological and biochemical evidence, elephant-shrews are included in an ancient African clade (superorder Afrotheria) that includes the paenungulates (elephants, hyraxes, and sea cows), aardvark, elephant-shrews, and afrosoricids (tenrecs and golden-moles—Madsen et al. 2001; van Dijk et al. 2000).

Petrodromus is derived from the Greek *petra* and *dromas* meaning "rock runner" (probably in reference to the mistaken idea that these mammals scamper over rocks), and *tetradactylus* is derived from the Greek *tetra* and *daktylos* meaning "four toes," in reference to the lack of a big toe on the hind foot. An uncommon, vernacular name for this species is the forest elephant-shrew (Nowak 1999). The name "elephant-shrew" should be hyphenated in order to distinguish this monophyletic group from the true shrews (Soricidae) in the order Insectivora (Rathbun 1995). Kingdon (1997), perhaps to avoid the association with true shrews, also calls elephant-shrews "sengis" (e.g., 4-toed sengi). Sengi, or very similar sounding words, is used for elephant-shrews in several Bantu-based languages in central and southern Africa, and Swahili speakers of coastal eastern Africa.

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LITERATURE CITED

Allen, G. M., and A. Loveridge. 1927. Mammals from the Uluguru and Usambara mountains, Tanganyika territory. Proceedings of the Boston Society of Natural History 38:413–441.

Ansell, A. D. H., and P. D. H. Ansell. 1969. *Petrodromus tetradactylus* at Ngoma. The Puku: Occasional Papers of the Department of Wildlife, Fisheries and National Parks, Zambia 5:211–213.

Ansell, W. F. H. 1960. Mammals of northern Rhodesia; a revised checklist with keys, notes on distribution, range maps, and summaries of breeding and ecological data. The Government Printer, Lusaka, Rhodesia.

Ansell, W. F. H. 1963. Additional breeding data on northern Rhodesian mammals. The Puku: Occasional Papers of the Department of Wildlife, Fisheries and National Parks, Zambia 1: 9–10.

Baillie, J., and B. Groombridge (eds.). 1996. 1996 IUCN red list of threatened animals. IUCN—The World Conservation Union, Gland, Switzerland.

Brown, J. C. 1964. Observations on the elephant shrews (Macroscelididae) of equatorial Africa. Proceedings of the Zoological Society of London 143:103–119.

Bruce, D. 1915. Trypanosomes and other parasites of animals in Nyasaland. Report of the Sleeping Sickness Commission of the Royal Society 16:203–207.

Bruorton, M. R. 1992. Elephant-shrews, twitching trunks and monogamous mates. African Wildlife 46:272–274.

Butler, P. M. 1956. The skull of *Ictops* and the classification of the Insectivora. Proceedings of the Zoological Society of London 126:453–281.

Butler, P. M. 1995. Fossil Macroscelidea. Mammal Review 25: 3–14.

Coldiron, R. W. 1977. On the jaw musculature and relationships of *Petrodromus tetradactylus* (Mammalia, Macroscelidea). American Museum Novitates 2613:1–12.

Corbet, G. B. 1974. Family Macroscelidae. Part 1.5. Pp. 1–6 in The mammals of Africa: an identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.

Corbet, G. B., and J. Hanks. 1968. A revision of the elephant-shrews, family Macroscelididae. Bulletin of the British Museum (Natural History), Zoology 16:45–111.

Corbet, G. B., and B. R. Neal. 1965. The taxonomy of the elephant shrews of the genus *Petrodromus,* with particular reference to the East African coast. Revue de Zoologie et de Botanique Africaine 71:49–78.

Crandall, L. S. 1965. The management of wild mammals in captivity. University of Chicago Press, Illinois.

de Balsac, H. H., and F. Bourlière. 1955. Ordre des Insectivores. Systématique. Pp. 1653–1697 in Traité de Zoologie. Volume 17, Fascicule 2 (P.-P. Grassé, ed.). Masson et Compagnie, Paris, France.

Downs, C. T. 1996. Renal structure, and the effect of an insectivorous diet on urine composition of southern African elephant-shrew species (Macroscelidea). Mammalia 60:577–589.

Downs, C. T., and M. R. Perrin. 1995. The thermal biology of three southern African elephant-shrews. Journal of Thermal Biology 20:445–450.

Evans, F. G. 1942. The osteology and relationships of the elephant

shrews (Macroscelididae). Bulletin of the American Museum of Natural History 80:85–125.

FITZGIBBON, C. D. 1995. Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. Mammal Review 25: 19–30.

FITZGIBBON, C. D. 1997. The adaptive significance of monogamy in the golden-rumped elephant-shrew. Journal of Zoology, London 242:167–177.

FITZGIBBON, C. D., H. MOGAKA, AND J. H. FANSHAW. 1995. Subsistence hunting in Arabuko-Sokoke Forest, Kenya, and its effects on mammal populations. Conservation Biology 9:1116–1126.

FOURIE, L. J., J. S. DUTOIT, D. J. KOK, AND I. G. HORAK. 1995. Arthropod parasites of elephant-shrews, with particular reference to ticks. Mammal Review 25:31–37.

GROOMBRIDGE, B. (ED.). 1993. 1994 IUCN red list of threatened animals. IUCN—The World Conservation Union, Gland, Switzerland.

HELLER, E. 1912. New races of insectivores, bats, and lemurs from British East Africa. Smithsonian Miscellaneous Collections 60: 1–13.

HOLLISTER, N. 1916. Description of a new genus and eight new species and subspecies of African mammals. Smithsonian Miscellaneous Collections 66:1–8.

HOLLISTER, N. 1918. East African mammals in the United States National Museum. Bulletin of the United States National Museum 99:1–94.

HOOGSTRAAL, H., C. G. HUFF, AND D. K. LAWLESS. 1950. A malarial parasite of the African elephant shrew, *Elephantulus rufescens dundasi* Dollman. Journal of the National Malaria Society 9:293–306.

KEYMER, I. F. 1971. Blood protozoa of insectivores, bats and primates in Central Africa. Journal of Zoology, London 163:421–441.

KINGDON, J. 1971. East African mammals; an atlas of evolution in Africa. Academic Press, New York 1:1–446.

KINGDON, J. 1974. East African mammals; an atlas of evolution in Africa. Academic Press, New York 2A:1–341 + xix.

KINGDON, J. 1997. The Kingdon field guide to African mammals. Academic Press, San Diego, California.

LOVERIDGE, A. 1922. Notes on East African Mammalia (other than horned ungulates) collected or kept in captivity 1915–1919, part 2. Journal of the East African and Uganda Natural History Society 5(17):39–69.

MADSEN, O., ET AL. 2001. Parallel adaptive radiations in two major clades of placental mammals. Nature 409:610–614.

MCKENNA, M. C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 55–85 in Phylogeny of the primates, a multidisciplinary approach (W. P. Luckett and F. S. Szalay, eds.). Plenum Press, New York.

NEUMANN, O. 1900. Die von mir in den Jahren 1892–1895 in Ost- und Central-Africa, speciell in den Massai-Ländern und den Ländern am Victoria Nyansa gesammelten und beobachteten Säugethiere. Zoologische Jahrbücher; Abtheilung für Systematik, Geographie und Biologie der Thiere 13:529–562.

NICOLL, M. E., AND G. B. RATHBUN. 1990. African insectivora and elephant-shrews. An action plan for their conservation. IUCN-SSC Action Plans for the Conservation of Biological Diversity 16:1–53.

NOWAK, R. M. 1999. Walker's mammals of the world. Sixth edition. The Johns Hopkins University Press, Baltimore, Maryland 2: 837–1936.

PATTERSON, B. 1965. The fossil elephant shrews (family Macroscelididae). Bulletin of the Museum of Comparative Zoology 133:295–335.

PERRIN, M. R. 1995. Comparative aspects of the metabolism and thermal biology of elephant-shrews (Macroscelidea). Mammal Review 25:61–78.

PETERS, W. C. H. 1846. Bericht über die zur Bekanntmachung geeigneten Verhandlungen Königlich Preussischen Akademic der Wissenschaften zu Berlin 11:257–259.

RAMAN, J., AND M. R. PERRIN. 1997. Allozyme and isozyme variation in seven southern African elephant-shrew species. Zeitschrift für Säugetierkunde 62:108–116.

RATHBUN, G. B. 1976. The ecology and social structure of the elephant-shrews *Rhynchocyon chrysopygus* Günther and *Elephantulus rufescens* Peters. Ph.D. dissertation, University of Nairobi, Kenya, 264 pp.

RATHBUN, G. B. 1979. The social structure and ecology of elephant-shrews. Advances in Ethology, Supplement to Journal of Comparative Ethology 20:1–77.

R[ATHBUN], G. B. 1984. Elephant-shrews, order Macroscelidea. Pp. 730–735 in The encyclopedia of mammals (D. [W.] Macdonald, ed.). Facts on File Publications, New York.

RATHBUN, G. B. 1995. Elephant shrews are not elephant-shrews. ITSES, Newsletter of the Insectivore, Tree-shrew, and Elephant-shrew Specialist Group, Species Survival Commission, IUCN—The World Conservation Union 2(1):5–6.

ROBERTS, A. 1913. The collection of mammals in the Transvaal Museum registered up to the 31st March, 1913, with descriptions of new species. Annals of the Transvaal Museum, Pretoria 4:65–107.

SHEPPE, W. A. 1973. Notes on Zambian rodents and shrews. The Puku: Occasional Papers of the Department of Wildlife, Fisheries and National Parks, Zambia 7:167–190.

SKINNER, J. D., AND R. H. N. SMITHERS. 1990. The mammals of the southern African subregion. Second edition. University of Pretoria, South Africa.

SMITHERS, R. H. N. 1986. South African red data book—terrestrial mammals. South African National Scientific Programmes Report 125:1–216.

SMITHERS, R. H. N., AND V. J. WILSON. 1979. Check list and atlas of the mammals of Zimbabwe Rhodesia. National Museums and Monuments, Zimbabwe Rhodesia, Salisbury, Museum Memoir 9:1–193.

SOKOLOV, V. E., A. A. DANKOVA, AND T. P. EVGEN'EVA. 1980. Morphology of the subcaudal specific cutaneous gland of the four-toed elephant shrew *Petrodromus tetradactylus*, Mammalia, Insectivora. Doklady Akademii Nauk SSSR 250:746–748.

SPRINGER, M. S., H. M. AMRINE, A. BURK, AND M. J. STANHOPE. 1999. Additional support for Afrotheria and Paenungulata, the performance of mitochondrial versus nuclear genes, and the impact of data partitions with heterogeneous base composition. Systematic Biology 48:66–75.

THOMAS, O. 1897. New African mammals. Proceedings of the Zoological Society of London 1897:430–436.

THOMAS, O. 1898. 2. On the mammals obtained by Mr. A. Whyte in Nyasaland, and presented to the British Museum by Sir H. H. Johnston, K. C. B.; being a fifth contribution to the mammal-fauna of Nyasaland. Proceedings of the Zoological Society of London 1898:925–939.

THOMAS, O. 1903. XXX—New African mammalia of the genera *Petrodromus, Dendromys, Mus,* and *Lepus.* The Annals and Magazine of Natural History, Series 7, 12:339–344.

THOMAS, O. 1910. IX—New African mammals. The Annals and Magazine of Natural History, Series 8, 5:83–92.

THOMAS, O. 1918. XLIII—Notes on *Petrodromus* and *Rhynchocyon.* The Annals and Magazine of Natural History, Series 9, 1:364–370.

THOMAS, O. 1919. On a small collection of mammals from Lumbo, Mozambique. Annals and Magazine of Natural History, Series 9, 4:29–34.

THOMAS, O., AND R. C. WROUGHTON. 1907. 3. The Rudd exploration of South Africa.—VII. List of mammals obtained by Mr. Grant at Coguno, Inhambane. Proceedings of the Zoological Society of London 1907:285–299.

TOLLIVER, D. K., L. W. ROBBINS, I. L. RAUTENBACH, D. A. SCHLITTER, AND C. G. COETZEE. 1989. Biochemical systematics of elephant shrews from southern Africa. Biochemical Systematics and Ecology 17:345–355.

TRIPP, H. R. H. 1971. Reproduction in elephant-shrews (Macroscelididae) with special reference to ovulation and implantation. Journal of Reproduction and Fertility 26:149–159.

TRIPP, H. R. H. 1972. Capture, laboratory care and breeding of

elephant-shrews (Macroscelididae). Laboratory Animals 6: 213–224.

VAN DIJK, M. A. M., O. MADSEN, F. CATZEFLIS, M. J. STANHOPE, W. W. DE JONG, AND M. PAGEL. 2000. Protein sequence signatures support the African clade of mammals. Proceedings of the National Academy of Sciences of the United States of America 98:188–193.

WENHOLD, B. A., AND T. J. ROBINSON. 1987. Comparative karyology of three species of elephant-shrew (Insectivora: Macroscelididae). Zeitschrift für Säugetierkunde—International Journal of Mammalian Biology 52:1–9.

WOODALL, P. F. 1987. Digestive tract dimensions and body mass of elephant shrews (Macroscelididae) and the effects of season and habitat. Mammalia 51:537–545.

WOODALL, P. F. 1991. An ultrastructural study of the spermatozoa of elephant shrews (Mammalia: Macroscelidea) and its phylogenetic implications. Journal of Submiscroscopic Cytology and Pathology 23:47–58.

WOODALL, P. F. 1995a. The male reproductive system and the phylogeny of elephant-shrews (Macroscelidea). Mammal Review 25:87–93.

WOODALL, P. F. 1995b. The penis of elephant shrews (Mammalia: Macroscelididae). Journal of the Zoological Society of London 237:399–410.

WOODALL, P. F., L. B. WOODALL, AND D. A. V. BODERO. 1989. Daily activity patterns in captive elephant shrews. African Journal of Ecology 27:63–76.

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