

# Orycteropus afer.

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## *Orycteropus C. Geoffroy, 1796*

*Orycteropus C. Geoffroy, 1796:102 (not E. Geoffroy). Type species Myrmecophaga afa, Pallas, by original designation.*

**CONTEXT AND CONTENT.** Order Tubulidentata, Family Orycteropodidae, Subfamily Orycteropodinae. The order Tubulidentata is the only mammalian order with a single extant species (Jones, 1984). The genus *Orycteropus* contains six or more extinct species in addition to the one extant species (Patterson, 1975, 1978).

## *Orycteropus afer (Pallas, 1766)*

Aardvark

- Myrmecophaga afa* Pallas, 1766:64. Type locality "Promontorio Bona Spei" (Cape of Good Hope, Republic of South Africa).  
*Orycteropus senegalensis* Lesson, 1840:225. Type locality Senegal.  
*Orycteropus aethiopicus* Sundevall, 1843:236. Type locality near Bahr-el-Abiad, Sennaaria, Sudan.  
*Orycteropus wertheri* Matschie, 1898:266. Type locality Hinterland of Bagamoyo, Tanganyika Territory.  
*Orycteropus haussanus* Matschie, 1900:102, 104. Type locality Haussaland, interior of Togo, West Africa.  
*Orycteropus erikssoni* Loennberg, 1906:1, pl. 1. Type locality Northern Congo.  
*Orycteropus leptodon* Hirst, 1906:383. Type locality Efulen, Cameroons.  
*Orycteropus afer*, W. Rothschild, 1907:506. Type locality former German Southwest Africa. First use of current name combination, referred to as *O. a. albicaudus*.

**CONTEXT AND CONTENT.** Context noted in generic summary. We follow Meester (1971) and list 18 subspecies:

- O. a. adametzi* Grote, 1921:126. Type locality Bamessing, northwestern Cameroons.  
*O. a. aethiopicus* Sundevall, 1843:236, see above.  
*O. a. afer* Pallas, 1766:64, see above.  
*O. a. albicaudus*, W. Rothschild, 1907:506, see above.  
*O. a. angolensis* Zukowsky and Haltenorth, 1957:126. Type locality Capangombe, west of Schella Mountains, southwestern Angola.  
*O. a. erikssoni* Loennberg, 1906:1, pl. 1, see above.  
*O. a. faradjus* Hatt, 1932:1. Type locality Faradje, Haut-Uele, Congo Belge.  
*O. a. haussanus* Matschie, 1900:102, 104, see above.  
*O. a. kordofanicus* W. Rothschild, 1927:512. Type locality Kordofan, Sudan.  
*O. a. lademanni* Grote, 1921:123. Type locality Wassi, north of Kondoia-Irangi, Masai Plains, Tanganyika Territory.  
*O. a. leptodon* Hirst, 1906:383, see above.  
*O. a. matschiei* Grote, 1921:122. Type locality Mikindani, south coast of Tanganyika Territory.  
*O. a. observandus* Grote, 1921:123. Type locality Ussangire, northwest of Ssongea, northwest coast of Lake Nyassa, Tanganyika Territory.  
*O. a. ruvanensis* Grote, 1921:123. Type locality Ruwana region, southwest coast of Victoria Nyanza, Tanganyika Territory.  
*O. a. senegalensis* Lesson, 1840:225, see above.  
*O. a. somalicus* Lydekker, 1908:466. Type locality Somaliland.  
*O. a. wardi* Lydekker, 1908:467. Type locality northeastern Rhodesia.  
*O. a. wertheri* Matschie, 1898:266, see above.

**DIAGNOSIS.** *Orycteropus afer* has a long snout, large ears, and long muscular tail. It is a medium sized piglike mammal with a stocky body, a short neck, and an arched back (Fig. 1). The forelimbs are short and powerful. Four toes are present on the forefoot, five

on the hind foot, with shovel-shaped unguis. The teeth are unique and consist of many fused minute dentine columns that appear as tubes on the growing base of the tooth. Teeth grow continuously, are without enamel, are covered with cement, and are rootless. The skull has an enlarged olfactory region with nine to 10 endoturbinals (highest number within Mammalia). The tympanic is horseshoe shaped and the lacrimal foramen is located at the facial flange and close to or on the suture of the lacrimal and jugal. The septomaxilla and interparietal are absent, the mesethmoid is present. The minor palatine artery and nerve enter the palate through a foramen in the posterior edge of the palate and there is no alisphenoid canal. The testes are inguinal, baculum absent, the uterus duplex (Coupin, 1926; Jones, 1984; Sonntag, 1925; Weber, 1928).

**GENERAL CHARACTERS.** The skin is thick and sparsely covered with bristly hair, light in color on the body (though usually stained by soil) and darker on the limbs. The head and tail are whitish (Smithers, 1983). Females are slightly smaller than males. In females, the head is lighter and the tail has a bright white tip (Kingdon, 1971). The following measurements (in mm) are compiled from Grassé (1955), Kingdon (1971), Rahm (1972), Lawlor (1976), Smithers (1983), and Nowak and Paradiso (1983): total length, 1,400 to 2,200; tail length, 443 to 710; length of hind foot, 225 to 280; length of ear, 130 to 240; height at shoulder, 600 to 650; body mass, 40 to 100 kg. The body temperature is variable and ranges from 32.2 to 34°C (McNab, 1984).

**DISTRIBUTION.** The present distribution of aardvarks (Fig. 2) is limited to subSaharan Africa. According to Frechkop (1946), the range of this species possibly extended into North Africa in historical times.

**FOSSIL RECORD.** The oldest known representative of the genus *Orycteropus* is from the lower Miocene of East Africa (18 to 19 mybp; Pickford, 1975), although its generic allocation is doubted (Patterson, 1975). The oldest occurrence in Asia is 13 to 14 mybp (J. C. Barry, personal communication). A skull of *Lepotomanis* Filhol from the Eocene to Oligocene Quercy-deposits in France tentatively is referred to the tubulidentates (Thewissen, 1985). Patterson (1975) created a separate subfamily for the subRecent *Plesiorycteropus* from Madagascar. An Eocene mandible of *Tubulodon taylori* from Wyoming was described as a tubulidentate by Jepsen (1932) and, based on this description, Colbert (1933) believed that Tubulidentata has its origin in North America. Following Simpson (1959), it is now accepted that *Tubulodon* is a palaeonodot.



FIG. 1. A female *Orycteropus afer* ("Miriam") in search of termites and ants. Photographed July 1978 by J. Shoshani near Lake Naivasha, Kenya.

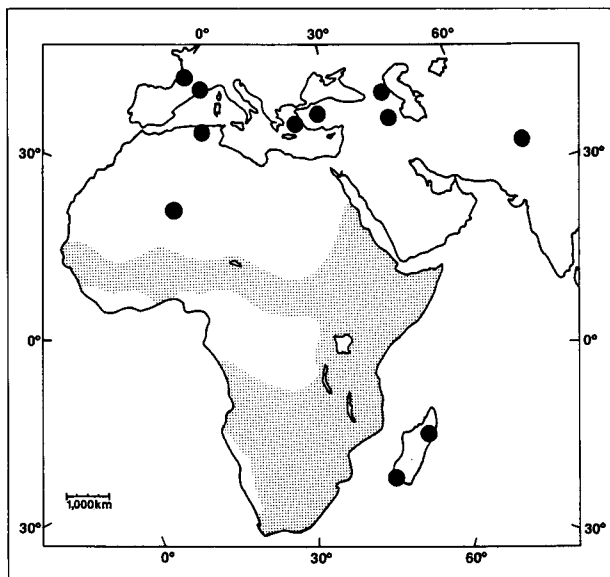


FIG. 2. Recent distribution of *Orycteropus afer* (shaded area) and localities of fossil tubulidentates outside of its recent range (black dots). Not all localities in Madagascar are indicated. Altered after Kingdon (1971), Patterson (1975), Pickford (1975), and Smithers (1983).

Tubulidentata probably evolved in Africa and is believed to be a condylarth derivative (Clark and Sonntag, 1926; MacInnes, 1956; Patterson, 1975).

**FORM AND FUNCTION.** The snout is elongated and the nostrils can be closed by means of hairs and muscular contraction (Pocock, 1924), an obvious adaptation to life underground. Sensory pads are located near the nostrils (Kingdon, 1971) and long hairs with a sensory function surround the eyes (Pocock, 1924). The hair of *O. afer* is  $17.9 \pm 3.6$  mm long (Buy and Koegh, 1984). It is yellowish-grey, with circular scale pattern, and large (distorted) oval or "egg-shape" in cross-section. The eyes are reduced; the animal is color blind and nocturnal (Franz, 1908; Jones, 1984). The pinnae are large and hearing is acute; the middle ear has a large tympanic membrane (Hunt and Korth, 1980). The mouth is small with a long and narrow tongue; neither lytta nor sublingua are present (Bender, 1909; Sonntag, 1923). Food particles are taken in with the tongue and scraped off by ridges on the palate as the tongue protrudes again (Eisentraut, 1976). The jaw muscles are weak (Frick, 1952, 1953) and the mandible is slender. The mandibular gland is enlarged and stretches down the neck to the clavicle.

The dental formula of an adult is  $i\ 0/0, c\ 0/0, p\ 2/2, m\ 3/3$ , total 20, and, although small additional teeth may be present, they do not erupt (Heuvelmans, 1939). According to Broom (1909a) the full dentition of *Orycteropus* is  $i\ 3/3, c\ 1/1, p\ 6/6, m\ 3/3$ , total 52, and the number of tiny premolars is variable but often exceeds the primitive mammalian number of four (Anthony, 1934; Heuvelmans, 1939). Patterson (1975) described, however, a fossil tubulidentate (*Leptorycteropus*) with an eutherian dental formula:  $i\ ?/? , c\ 1/1, p\ 4/4, m\ 3/3$ . Individual teeth are hypsodont (Anthony, 1934); M2 is the largest. The initial cusps wear off immediately (Heuvelmans, 1939), leaving two flat planes that meet at a low angle on all molars. Tubules that compose the teeth are elongated canals perpendicular to the occlusal plane (Fig. 3), with a wall of dentine and a diameter of approximately 0.2 mm (MacInnes, 1956); they number about 1,500 for the largest tooth (Jones, 1984). The canals do not enclose Tomes fibers, but are homologous to pulp-canals. In deciduous and immature teeth, the tubules occur in a homogenous matrix of cementum, but in adults they are tightly packed (MacInnes, 1956). Mastication of insects is reported by Kingdon (1971), but Patterson (1975) suggests that the essential function of the teeth is in mastication of fruits of *Cucumis humifructus*.

On the skull (Fig. 4) there is no sagittal crest or postorbital bar, but only a superior postorbital process with one large (frontal emissary) foramen anterior and ventral to it. There is no separate interparietal bone, and many foramina are present on the dorsal

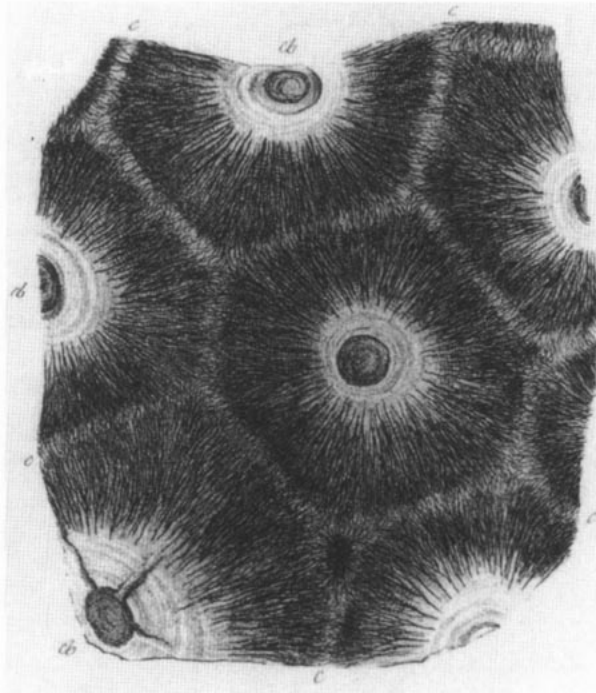


FIG. 3. Microstructure of a transverse section of a molar of *O. afer*,  $\times 300$  (after Duvernoy, 1853), showing "tubules" characteristic of Tubulidentata; "c" is a white line that forms at the common limit of two prisms; "cb" is the cavity (bulb) of each dentary prism.

aspect of the cranium. The zygomatic arch is complete but slender, and the jugal does not participate in the mandibular fossa, but is in contact with the lacrimal. A strong postpalatine torus is present; the posterior palatine foramina are at its caudal and lateral corners. The optic foramen and foramen ovale are separate but the orbital fissure and foramen rotundum are confluent. There is no alisphenoid canal. The sinus canal is present, the internal carotid foramen perforates the basisphenoid, and the hypoglossal canal is not confluent with the jugular foramen. A mastoid foramen is present; the foramen magnum is formed by the basioccipital, the exoccipitals, and the supraoccipital. The hyoid apparatus is composed of nine bones. The dentaries (Fig. 4) are slender and not fused, all three processes are distinct, and the condyle is directed anteroposteriorly. On the lateral side of each dentary, there are two or more mental foramina and the medial mandibular foramen is located dorsal to an imaginary line drawn on the level of the molar alveoli (Clark and Sonntag, 1926; de Beer, 1937; Grassé, 1955; Shoshani, 1986).

The cartilages of the organ of Jacobson are primitive (Broom, 1909b) and the olfactory chamber is enlarged; olfaction is a major sensory modality. The ectotympanic is horseshoe shaped and the ventral wall of the middle ear is largely unossified though minor ossifications may occur (Thewissen, 1985). A large epitympanic sinus is present, the internal carotid artery is in the promontory position, and the superior ramus of the stapedia artery is present. In the brain, the rhinencephalon is large (Friant, 1960; Sonntag and Woolard, 1925) and few and variable fissures are present on the neopallium (Pirlot and Kamiya, 1983; Thewissen, 1985).

The vertebral formula is  $C\ 7, T\ 13, L\ 8, S\ 6, Ca\ 25$  to 28, total 62 to 65 (Clark and Sonntag, 1926; Jones, 1984) and vertebrae are without supernumerary zygapophyses (xenarthrism), but caudal vertebrae possess chevron bones (hemal arches) on their ventral side. There are five sternebrae but no floating ribs (Fig. 5). The stomach is simple, with a strong *muscularis* (Allison, 1947), working as "a kind of gizzard" (Sonntag, 1925:400). Two azygous veins enter the heart separately (Beddard, 1909; Sonntag, 1925).

Digging burrows is done by means of flexion and extension movements of the arm. The powerstroke involves flexion of the shoulder, elbow, and metacarpophalangeal joints, but not of the wrist. Pronation and supination are limited. The muscles used in digging are flexors of the shoulder, extensors of the elbow, and flexors of

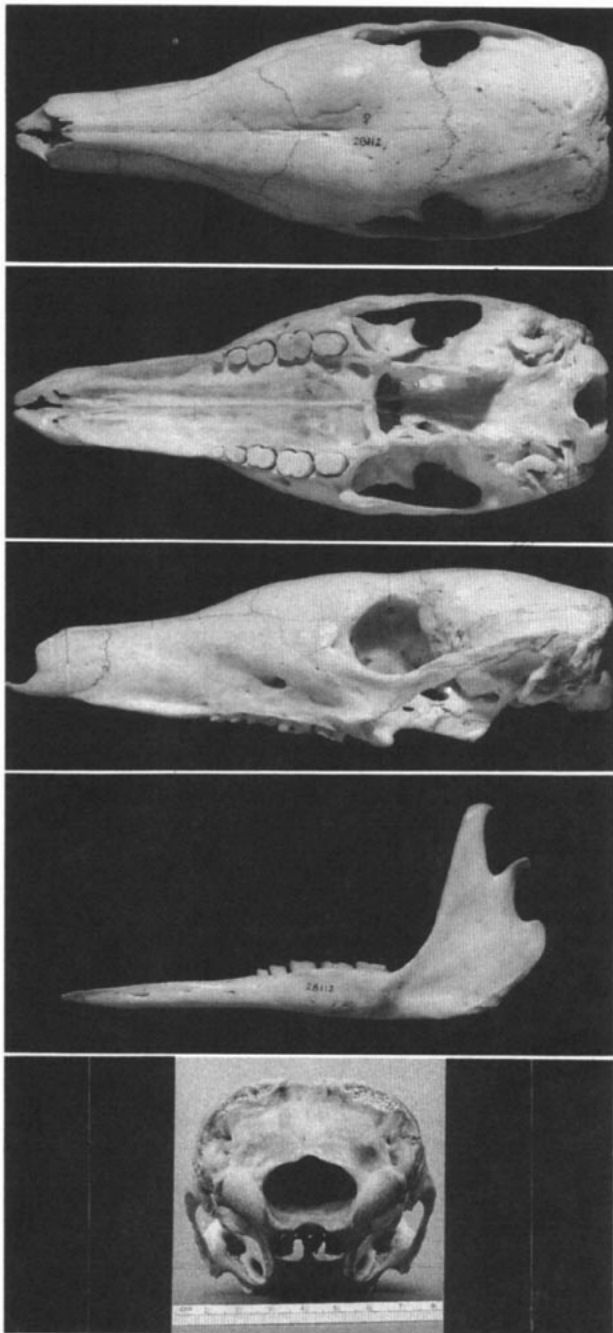


FIG. 4. Dorsal, ventral, and lateral views of the cranium, and lateral view of the dentary of *Orycteropus afer* (zygomatic breadth is 83.5 mm; ROM 28112, female from Athi River, near Nairobi, Kenya) and posterior view of cranium of AMNH 150398. Photographs (top four) by E. Knapp, (bottom) by J. Shoshani.

the hand (Thewissen and Badoux, 1986). All four digits are used in digging, and are about equally thick, but differ in length (Frechkop, 1937). The ungues are strong, and resemble both nail and hoof (Jones, 1984; Pagès, 1970). In the forelimb, the clavicle is present and strong (Fig. 5), the humerus has a strong entepicondyle with a foramen, the ulna has a large olecranon and is as stout as the radius, the carpal bones are arranged alternately, and the metacarpals are about as long as the proximal phalanges. In the hind limb, the femur has a third trochanter, the tibia and fibula are fused proximally, the tarsus is serial (astragalus does not articulate with cuboid), and there is an astragalar foramen. According to Grassé (1955) only the digits touch the surface when the animal is walking. The track illustrated by Smithers (1983) appears to confirm this hypothesis. At rest, the forefoot is digitigrade and the hind foot is plantigrade.

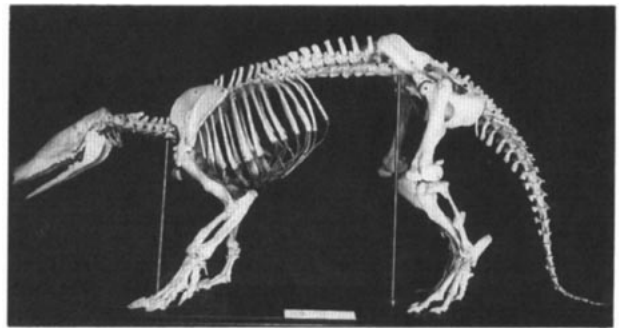


FIG. 5. Skeleton of a male *Orycteropus afer erikssoni*, AMNH 51375 from Congo (=Zaire), 3 December 1913. Scale is 152 mm; measurements in mm are: total length = 1,980, tail length = 760, length of hind foot = 300. Photograph by J. Shoshani.

Placentation is zonary, endotheliochorial, and a four-lobed allantois with a marginal hematoma is present (Horst, 1949; Perry, 1974). There are two pairs of mammae, one abdominal and one inguinal (Grassé, 1955). Both males and females have scent glands in the genital region (Pocock, 1924).

Blood-chemistry data available from a captive male specimen are: packed cell volume, 34 volume percent; hemoglobin, 12.5 g/dl; red blood cells,  $2.18 \times 10^6/10^{-6}$  l; mean corpuscular volume,  $155.9 \times 10^{-15}$  l; mean corpuscular hemoglobin,  $57.3 \times 10^{-12}$  g; mean corpuscular hemoglobin content, 37%; and white blood cells,  $2.86 \times 10^3/10^{-6}$  l. The periphery arterial rate (PAR) of a captive female aardvark ranged from 74 to 88 beats/min, and of eight measurements, 84 PAR seems the most reliable (taken as animal ate in a standing position). During the 2-h observation, the ambient temperature ranged between 20 and 21.1°C and the animal's body temperature (Tb), measured four times at the axillary regions, ranged between 32.2 and 33.6°C. According to McNab (1984) the Tb of *O. afer* is 34.5°C and the lower limit of thermoneutrality is 27.0°C. The basal metabolic rate (in ml  $O_2 g^{-1} h^{-1}$ ) of *O. afer* is  $0.128 \pm 0.002$ . This low rate of metabolism is related directly to low Tb and generally is associated with a myrmecophagous adaptation (McNab, 1984).

**ONTOGENY AND REPRODUCTION.** Polygamy seems probable because males are thought to (1) associate with females only during the breeding season (Fitzsimons, 1920), and (2) wander more than females (Dorst and Dandelot, 1969).

Estrus is characterized by vaginal swelling and sometimes a discharge. Observations of copulation have not been reported. There are few signs of pregnancy as most animals usually are pot-bellied. During pregnancy, the abdomen and mammae are enlarged; milk can be expressed 1 month before birth (Goldman, 1986; Jacobi, 1972). Aardvark milk is composed of 68.3% water (with dissolved elements), 14.6% protein, 11.9% fat, 3.8% carbohydrate, and 1.5% ash (Kisling and Sampsell, 1976; White et al., 1985).

Gestation is thought to approximate 7 months. One young is born, occasionally two (Goldman, 1986; Verheyen, 1951). Nothing is known of early stages of embryo development. Taverne and Bakker-Slotboom (1970) described the placenta and fetal membranes. A specimen with one fetus had two corpora lutea present in the right ovary and three in the left, all seemed histologically to belong to the same gestation (Asdell, 1964). Lasley (1977) described a technique to determine the sex of a neonate by everting the genital opening and examining the underlying structures.

Births in the wild have been reported from May to July in South Africa (Fitzsimons, 1920); May to August in Botswana (Smithers, 1971); October to November in Zaire (Verheyen, 1951); early November in Uganda (Kingdon, 1971); and May to June in Ethiopia (Rahm, 1972). Births in central Africa reportedly occur at the beginning of the second rainy season from October to November (Verheyen, 1951). Births in captivity have been reported for all months of the year with peaks in February, March, and June (Goldman, 1986).

At birth, naked flesh-colored young weigh 1.8 to 2 kg, and have a total length of approximately 550 mm (Haltenorth and Diller, 1977). In the neonate, both eyes are open, there are no visible signs of teeth, and the claws are well developed (Cullen, 1967). At 1

month, young weigh 3.5 kg, with a total length of 680 mm; at 3 months, 9 kg, 930 mm; and at 7 months, 33 kg, 1,200 mm (Haltenorth and Diller, 1977). Young remain in the burrow for 2 weeks after birth before accompanying the female on nocturnal forays, dig their own burrow at 6 months, and remain with the female until the next mating season (Verheyen, 1951). A captive young buried feces at 2 weeks, had erupted teeth at 12 weeks, was first observed to eat ants at 14 weeks, and weaned at 16 weeks (Sampson, 1969). Hair growth is visible at 5 to 6 weeks. Young attain the size of an adult at about 12 months (Jacobi, 1972).

Sexual maturity is attained at about 2 years (Haltenorth and Diller, 1977). The youngest captive female to give birth was 3 years of age, thus having conceived when at least 2 years 5 months old. During a period of 16 years in captivity, a female gave birth to 11 young, and a male sired 18 offspring by 24 years of age (Goldman, 1986).

**ECOLOGY.** The aardvark is preyed upon by lions, *Panthera leo*, leopards, *Panthera pardus*, cheetahs, *Acinonyx jubatus*, hunting dogs, *Lycaon pictus*, and pythons, *Python sebae*, but man and hyaenas, *Crocuta crocuta*, are considered the most notable predators (Kingdon, 1971). Hyaenas and pythons frequently consume young, sometimes in burrows (Fitzsimons, 1920). Aardvark burrows are used for shelters or breeding sites by many small and medium-sized vertebrates (Melton, 1976; Rahm, 1972; Smithers, 1971). Okiwelu (1977) observed that the tsetse fly *Glossina m. morsitans* uses aardvark burrows for resting sites. In some regions, the prevalence of warthogs *Phacochoerus aethiopicus* depends on the number of abandoned aardvark burrows (Melton, 1976; Rahm, 1972). Burrows of *O. afer* provide protection for many animals from bush fires (Rahm, 1972).

An association exists between *O. afer* and a species of wild cucumber, *Cucumis humifructus*, known in South Africa as the "aardvark pumpkin." The round whitish fruits of this plant develop 20 to 30 cm below the ground surface and it is assumed that the aardvark digs for the fruits in search of moisture, as these fruits are ripe during the driest months of the year. Only the aardvark can dig and eat the buried fruits; thus, the aardvark disseminates the seeds when it buries its feces (Meeuse, 1959; Mitchell, 1965; Verheyen, 1951).

Ectoparasites of *O. afer* include ticks (Acarina) *Haemaphysalis muhsami* (Clifford and Anastos, 1962), *Hyalomma impressum* (Wilson, 1950), *Rhipicephalus cuspidatus* (Morel and Mouchet, 1958; Osman, 1978), *R. longus* (Clifford and Anastos, 1962), *R. lunulatus* (Travassos Santos Dias, 1955), *R. masseyi* (Clifford and Anastos, 1962), *R. reichenowi* (Clifford and Anastos, 1962; Walker, 1966), *R. sanguineus* (Wilson, 1950), *R. s. sanguineus* (Travassos Santos Dias, 1955; Zumpt, 1958), *R. simus* (Clifford and Anastos, 1962; MacLeod, 1970; Wilson, 1950), *R. s. simus* (Travassos Santos Dias, 1952), and *R. tricuspidatus* (Clifford and Anastos, 1962; Zumpt, 1958); sucking lice (Anoplura) *Haematopinus notophallus* (Neumann, 1909) and *Hybophthirus notophallus* (Bedford, 1926; Cummings, 1916; Ferris, 1922; Waterston, 1914); a flea (Siphonaptera) *Echidnophaga larina* (Bedford, 1926; Haeselbarth et al., 1966; Jordan and Rothschild, 1906; Waterston, 1914); and flies (Diptera) *Aucheromyia* sp. (Askew, 1971), *Neocordylobia roubaudi* (Zumpt, 1967), and *Pachychoeromyia praegrans* (Askew, 1971).

Endoparasites of *O. afer* include flagellates (Mastigophora) *Trichomonas* sp. (MacKinnon and Dibb, 1938), *Trypanosoma brucei* (Neves, 1971), and *T. rhodesiense* (Burt, 1946); an amoeba (Sarcomastix) *Entamoeba* sp. (MacKinnon and Dibb, 1938); the thorny-headed worm (Acanthocephala) *Nephridiicanthus longissimus* (Golvan, 1962; Schmidt and Canaris, 1967); round worms (Nematoda) *Ancylostoma hescheleri* (Moenig, 1938), *Angulocirrus ocyteropi* and *A. minor* (Biocca and Le Roux, 1957), *Capillaria* sp. (Fox, 1940), *Dirioflaria* sp. (Dieterich, 1978), *Filaria martis* (Le Roux, 1950), *Gendrespirura chabaudi* (Le-Van-Hoa, 1962), *G. hamospiculata* (Vulsteke, 1956), *Gongylonema congolense* (Fain and Thienpont, 1958), *Physaloptera* sp. (Stossich, 1900), and *Trichinosis spiralis* (Fox, 1940); and a pentastome (Porocephalida) *Armellifer armillatus* (Doucet, 1960; Zumpt, 1961).

No infectious diseases specific to *O. afer* have been reported. Diseases and ailments of captive animals include arteriosclerosis, bronchitis, conjunctivitis, dermatitis, fecal impaction, intestinal abscesses, osteomyelitis, peritonitis, pneumonia, salmonellosis, umbilical

hemorrhage, and umbilical stalk infection (Bohorquez and Stout, 1972; Dieterich, 1978; Goldman, 1986).

Aardvarks dig burrows for food, as temporary shelters, and for permanent residence (Melton and Daniel, in press; Smithers, 1983). Food burrows vary from a deep hole covering the animal completely to one that is only sufficiently deep to cover the animal's head. Temporary burrows serve as refuges for only a few days, based upon evidence from spoor. Inactive termite mounds also are used as temporary shelters. If too far from its permanent burrow by dawn, aardvarks excavate temporary sleeping burrows (Haltenorth and Diller, 1977). In permanent burrows, animals take up residence and bear young. Typical burrows are 2 to 3 m long (Verheyen, 1951) with one entrance, but may include single straight tunnels and extensive tunnel systems with many access holes. Of 25 described burrow systems, 15 had one entrance, 6 had two, 3 had three, and 1 had five (Melton, 1976). Roberts (1951) counted 60 burrow entrances in an area not more than 274 by 90 m. The entrance may be concealed beneath shrubs or in long grass and can be located because of more dense vegetation located around the opening, owing to rich subsoil thrown out by the occupant (Fitzsimons, 1920). The entrance usually is the narrowest part of a burrow measuring about 40 to 50 cm in diameter (Melton, 1976). Three of five excavated burrows ended in a round chamber where an animal slept; two of these chambers measured 1 m wide by 80 cm high, permitting the animal to turn around and exit the burrow head first. No special sleeping accommodations are found in sleeping chambers except loosened dirt (Rahm, 1972). Kingdon (1971) excavated a burrow that had been tunnelled about 6 m below the ground surface. Tunnels descending at a 45° angle have been reported (Rahm, 1972). Burrows occasionally are dug in areas that flood seasonally, thus may have to be evacuated at certain times of the year (Smithers, 1971).

The diet of *O. afer* consists mainly of ants (Formicidae) and termites (Isoptera). Termites are taken mainly during the wet season and ants during the dry season, probably related to the quiescent nature of termites in the dry season (Melton, 1976; Smithers, 1983). Termites taken include *Macrotermes*, *Allodontotermes*, *Basiditermes*, *Cubitermes*, *Hodotermes*, *Microhodotermes*, *Odontotermes*, *Pseudocanthotermes*, and *Trinervitermes* (Kingdon, 1971; Melton, 1976; Rahm, 1972; Smithers, 1983; Van Ark, 1969). Ants taken include *Alaopone*, *Anopolepis*, *Camponotus*, *Crematogaster*, *Dorylus*, and *Typhlopone* (Smithers, 1983). Rahm (1972) noted that an aardvark cannot fully satisfy its hunger from breaking open termite mounds, thus must find termite colonies making mass movements on the ground. A specimen was collected in Botswana while it was masticating two fat mice, *Steatomys pratensis* (Smithers, 1971), an occurrence considered unusual by Smithers (1983). Kingdon (1971) reported that one stomach contained over 40 scarabaeid pupae eaten in a single night and that locusts (family Acrididae) occasionally are eaten. During the dry season, aardvarks also take fungi from termite "fungus gardens," and grasshoppers (Acrididae), grubs, and other insects (Haltenorth and Diller, 1977). Melon seeds have been recorded in stomach contents (Smithers, 1983). Stomach contents invariably contain a high percentage of soil, sand, small stones, and other debris ingested with food; in a specimen from Botswana, debris accounted for 47% of the stomach contents by weight (Smithers, 1971). Aardvarks drink water; completely arid conditions cannot be tolerated (Kingdon, 1971; Verheyen, 1951). Watering holes are visited frequently (Rahm, 1972).

Aardvarks can be of economic importance to man by controlling termite numbers. In parts of South Africa where the aardvark and many other insectivorous mammals and birds have been exterminated, pasture and cereal crops have suffered enormous depredation from certain termites that may remove over 60% of the standing crop in dry years (Kingdon, 1971). Grazing by wild ungulates and domestic stock creates suitable conditions for aardvarks by producing trampled surface vegetation and dry dung that attracts termites (Kingdon, 1971). Aardvark burrows often damage farmland and are obstacles to moving vehicles and galloping horses (Fitzsimons, 1920; Melton and Daniel, in press; Roberts, 1951; Smithers, 1983).

The aardvark was hunted frequently by Bushmen, Hottentots, and colonists for its flesh, hide, or strictly for sport (Fitzsimons, 1920). The flesh is prized by some natives and has the appearance of coarse beef (Nowak and Paradiso, 1983) and a taste much like pork (Melton, 1976). Many parts of the aardvark have been used as charms and curios: teeth (prevent illness and bring good luck),

claws (catch termites and as a hoeing charm), bristly hair (poison ingredient), and snout and digits used by witch doctors (Kingdon, 1971; Melton, 1974; Smithers, 1983). Images of armadillo appear regularly in modern rock paintings (Woodhouse, 1984).

*Orycteropus afer* was listed on 1 July 1975 under Appendix II of CITES; an export permit is required from the country of origin before a live animal or its parts or derivatives can be imported into a member nation. This species is listed not because of scientific information of its threatened status but rather because of a lack of information (Melton, 1976).

Most zoos house *O. afer* in pairs in nocturnal exhibits. Captive diets for adult animals consist of meat, eggs, milk, and cereals with vitamin and mineral supplements. Of 58 births in zoos reported between 1962 and 1980, at least 63% died in infancy. After most captive births, females have shown either minimal or no interest in tending offspring; hand-rearing has been necessary. Longevity in captivity is at least 24 years (Goldman, 1986).

When isolated from its burrow the armadillo is captured easily, but because of its enormous strength several men are required to capture an adult in the wild (Fitzsimons, 1920). They can strike powerful blows with their shoulders by making rapid and sudden turning movements. Fitzsimons (1920) reported that a man's leg was broken in this manner. According to Smithers (1983), "toggled snares" are used successfully to trap armadillos in their permanent burrows; "heavy drag weights" also must be used. Chemical restraint has been used successfully to immobilize adult animals in captivity; a 56.7 kg male received 600 mg of ketamine hydrochloride and 15 mg of diazepam (Goldman, 1986); ketamine hydrochloride (2.5 to 4.5 mg/kg) and droperidol (20 mg/ml) combined with fentanyl (0.4 mg/ml) at a dosage of 0.15 mg/kg of fentanyl also have been used (Dieterich, 1978).

**BEHAVIOR.** The armadillo is nocturnal, possibly territorial, and usually solitary. Both sexes spend most of the year in separate burrows, but where densities are high, several animals may meet and feed in the same area (Kingdon, 1971). Females may be seen with young of previous years (Verheyen, 1951). Within its territory, a resident animal uses the same paths at regular intervals of about 1 week and frequents the same termite hills (Rahm, 1972). When foraging, an armadillo travels in a zig-zag path with its snout to the ground inspecting a strip about 30 m wide. The ears are directed forward and slightly to the side. When digging or moving rapidly, armadillos frequently stop and hold their snouts pressed to the ground and sniff, often vigorously (Melton, 1976; Walter, 1981). Kingdon (1971) suggested that fleshy tentacles around the nostrils may be highly sensitive to chemical and mechanical (moving ants and termites) stimuli. Hearing is thought to be essential as the animals have been observed to forage with their heads raised (Melton, 1976). While foraging, animals may make many excavations around the base of termite mounds, destroy mounds by a single large burrow into their centers at ground level, or dig into subterranean ant and termite nests away from mounds. *O. afer* can cause considerable damage to a termite mound, including the destruction of the nest (Lepage, 1984). A typical dig is only 20 to 40 cm deep and made in less than 20 s. The average time feeding at a typical dig is 1 min. Estimates of total foraging distance average about 10 km per night, with a maximum of 30 km (Kingdon, 1971; Melton, 1976; Verheyen, 1951). Two individuals tracked in the Transvaal foraged over distances ranging from 2 to 5 km/night (van Aarde, 1984).

Armadillos dig with their front claws and displace the matrix with the hind feet and tail (Fitzsimons, 1920; Patterson, 1975). They easily can excavate the cementlike wall of a termite mound, that often is so hard a man with a pickaxe cannot break into one. Van Ark (1969) reported that *O. afer* was responsible for an average mortality of 18.9% of mounded *Microhodotermes viator* colonies. A 1-m burrow can be dug in 5 min (Melton, 1976). While digging, the ears are folded downwards and the vertical slits of the nostrils tightly closed (Kingdon, 1971).

*Orycteropus afer* captures its prey by inserting its long protractile tongue amongst ants and termites and drawing it back into the oral cavity. The tongue can be thrust 250 to 300 mm out of the mouth (Kingdon, 1971). Food is swallowed after being masticated only a few times (Fitzsimons, 1920).

When an animal is caught it quickly tucks its head between its forelegs and performs a somersault with great speed, while kicking viciously with its hind legs and sharp claws (Ranger, 1968). It avoids

enemies by digging or seeking refuge in a burrow (Nowak and Paradiso, 1983). The armadillo is reported to swim readily (Rahm, 1972), have poor vision (Melton, 1976), and be almost blinded by light (Dorst and Dandelot, 1969). In an aggressive encounter, *O. afer* may strike with its tail or forelimbs, rear on its hind legs and slash with the forefeet, or roll on the back and slash with all feet (Nowak and Paradiso, 1983). If an attempt is made to excavate an armadillo from its burrow, it will dig rapidly, blocking the passage behind it at about 2-m intervals (Kingdon, 1971).

Armadillos sleep during the day curled in a tight circle with the snout covered by the tail and hind feet (Kingdon, 1971). According to Smithers (1983), armadillos appear to sleep soundly. Bushmen in Botswana spear them as the animals lie sleeping in the sun at burrow entrances. Before resting in the burrow it blocks the burrow entrance, leaving a small opening at the top (Kingdon, 1971). Hediger (1951) suggested that there may be a partial arrest of circulation to accommodate the lack of oxygen in deeper tunnels. Armadillos exit burrows in a typical manner: after pausing at the burrow entrance for several minutes they move suddenly for about 12 to 20 m before pausing again to sense their surroundings. *O. afer* basks in the sun for short periods at the burrow entrance (Kingdon, 1971; Melton, 1974; Smithers, 1983; Verheyen, 1951).

Armadillos bury their feces in a consistent manner. The droppings are ovoid cakes that average 4 cm in length (Kenmuir and Wilson, 1975) and are covered by a musty-smelling green secretion. As much as 0.5 kg may be deposited at one time in a shallow hole about 10 cm deep, and subsequently covered with soil (Melton, 1976). This behavior may contribute to avoidance or attraction of other individuals of the same or other species.

When walking and upon entering a burrow, *Orycteropus afer* makes a muffled grunt. Any sudden fright or what appears to be pain is accompanied by a bleating calflike bellow. When foraging they sniff vigorously (Kingdon, 1971). The armadillo is among several mammals prone to stereotyped patterns of movement in captivity such as pacing (Boorer, 1972).

**GENETICS.** Benirschke et al. (1970) reported a diploid chromosome number of 20 for *O. afer*; the karyotype has two pairs of large subtelocentric chromosomes, seven pairs of medium to small metacentric and submetacentric autosomes, a small metacentric X and a small biarmed Y chromosome. The nuclei of *O. afer*, according to Benirschke et al. (1970), have 1.673 times more DNA than human nuclei. Pathak et al. (1980) reported that all chromosomes of *O. afer* possess centromeric C-bands, and that all chromosome pairs can be identified unequivocally by G-banding. The mucosal epithelial cells of a female armadillo contain typical nuclear Barr bodies (Lasley, 1977).

**REMARKS.** Sherborn (1902:701) gives "*Orycteropus Geofroy*, Decad. Phil. et litt. XXVIII. 1795."; however, neither Sherborn nor we were able to trace this reference and used the 1796 citation instead. "Tubulidentata" refers to the microstructure of the molars; "*Orycteropus*" means "burrowing foot" and "*afer*" is an adjective form of Africa. "Armadillo" is derived from the Dutch (through Afrikaans) and means "earth pig" (Bertin and Burton, 1967; Duvernoy, 1853). The armadillo also is commonly known as the anthear (Smithers, 1983).

Seventeen subspecies of *O. afer* were listed by Allen (1939) and 18 by Meester (1971); however, their validity and geographic ranges are unknown. *O. afer* differs from most species now placed in Edentata by number and structure of teeth, absence of septomaxilla, presence of mesethmoid, structure of bullae, stapes, internal choanae, certain cranial foramina, and certain characters of the astragalus. Nevertheless, until the turn of the 20th century, Tubulidentata was placed in Edentata together with Pholidota and Xenarthra (Simpson, 1945). It was given ordinal rank by Huxley (1872) and placed in the superorder Protungulata by Simpson (1945). Simpson's (1945) Paenungulata includes the extant orders Proboscidea, Sirenia, and Hyracoidea plus four extinct orders. McKenna's (1975) grandorder Ungulata essentially embraces Ungulata and Paenungulata. Biochemical evidence for close relationship of Tubulidentata to Paenungulata was provided by de Jong et al. (1981) and Shoshani et al. (1981). Dene et al. (1983:1585) concluded that *Orycteropus* lineage is "... one of the most ancient among Eutheria." Affinities of Tubulidentata to paenungulates were challenged on morphological grounds by Thewissen (1985). Shoshani (1986),

based on nondental osteological characters, placed Tubulidentata close to Notoungulata, Artiodactyla, and Perissodactyla.

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