

Vulpes zerda. By Serge Larivière

Published 26 December 2002 by the American Society of Mammalogists

Vulpes zerda (Zimmerman, 1780)

Fennec

- Vulpes minimus* Skjöldebrand, 1777:267. Type locality “Saara . . . Alger” (Algerian Sahara).
- Canis zerda* Zimmerman, 1780:247. Type locality “Es bewohnt die Soara und andere Theile von Nordafrika hinter den Atlas, der Ritter Bruce behauptet, man fände es auch in tripolitanischen.” (inhabits the Sahara and other parts of North Africa behind the Atlas, Ritter Bruce alleges that it can also be found within Tripolitani).
- Canis cerdo* Gmelin, 1788:75. Type locality “Africae . . . Saara” (Sahara, Africa).
- Viverra aurita* Meyer, 1793:91. Type locality Biskra, Beni Mezzab and Weryleh, Algeria vide Kowalski and Rzebik-Kowalski 1991 (see remarks).
- Fennecus arabicus* Desmarest, 1804:18. No locality specified.
- Megalotis cerda* Illiger, 1811:131. Based on *Canis cerdo* Gmelin.
- Fennecus brucei* Desmarest, 1820:235. Type locality “Libya, Tunis, Algeria, Sennaar.”
- Canis fennecus* Lesson, 1827:168. Based on *Canis zerda* Zimmerman.
- Vulpes denhamii* Boitard, 1842:213. Type locality “interior of Africa.”
- Vulpes zaarensis* J. E. Gray, 1843:62. Type locality “Egypt.”
- Canis saharensis* Leuck. via Gray, 1843:62. Listed by Gray without comment.
- Canis pygmeus* Leuck. via Gray, 1843:62. Listed by Gray without comment.
- Vulpes zerda* Corbet, 1978:164. First use of current name combination.

CONTEXT AND CONTENT. Order Carnivora, family Canidae, genus *Vulpes*. The fennec has been classified under the genus *Canis* (van Gelder 1978) or in its own genus *Fennecus* (Ellerman and Morrison-Scott 1966; Nowak 1991; Tedford et al. 1995). First use of the name *F. zerda* is not clear. Molecular data suggest the fennec is within *Vulpes* (Wayne et al. 1997). Its closest relative is the Blanford fox, *Vulpes cana*, and both species probably diverged ca. 4–4.5 million years ago (Geffen et al. 1992b; cf. Clutton-Brock et al. 1976). *V. zerda* is monotypic.

DIAGNOSIS. The fennec (Fig. 1) is a small member of the Canidae (Kingdon 1990; Sheldon 1992). It differs from the sympatric Rueppell’s sand fox (*V. rueppelli*) by its smaller size (body mass <1.5 kg versus ca. 2 kg in Rueppell’s sand fox); paler, shorter, and finer fur; shorter and black-tipped tail (50% of head and body length versus 70% with white tip in *V. rueppelli*); shorter legs; and larger ears (Gasperetti et al. 1985; Harrison 1968). Skull of *V. zerda* differs from that of *V. rueppelli* by its smaller size, smoother surface, inflated braincase, and larger tympanic bullae (Harrison 1968). The fennec, *V. zerda*, can be differentiated from the Blanford’s fox, *V. cana*, because the latter has a tail >20% longer and a hind foot ca. 3% shorter than those of the fennec (Geffen et al. 1992a).

GENERAL CHARACTERS. The fennec is a small (ca. 1.0 kg) fox with large ears (ca. 10 cm in length) and a small muzzle. Height at the shoulder is 20 cm, and total length rarely exceeds 60 cm (Gauthier-Pilters 1967). Pelage is long, woolly, soft, and pale. Underfur is ca. 28 mm in length (Harrison 1968). Head is whitish with an indistinct brown patch in front of eyes. Eyes are black and large. Ears are white inside and cinnamon rufous outside; central part of ear is nearly naked internally and covered with short, very fine hairs elsewhere (Harrison 1968). Flanks, underparts, and limbs are almost white. Rufous tail is short (ca. 215 mm), bushy, thick, and often has a black patch near the dorsal base as well as a black

tip (Dorst and Dandelot 1970). Hair on tail is ca. 35 mm. Limbs of individuals from North Africa are reddish-sand in color, whereas those from individuals farther south are nearly white (Sheldon 1992). Pads are completely covered with hairs up to 13 mm in length (Harrison 1968). Measurements (in mm) of 1 male from Kuwait are: total length, 583; length of tail, 215; length of hind foot, 96; length of ear, 97 (Harrison 1968). Measurements (in mm) of 1 female from Libya are: total length, 578; length of tail, 210; length of hind foot, 103; length of ear, 100 (Hufnagl 1972). Measurements (in mm) of 1 male and 3 females (range of females in parentheses) born in captivity from North African parents (Mendelssohn and Yom-Tov 1987) are: length of body, 402, 390 (not recorded); length of tail, 214, 202 (178–215); length of ear, 110, 92 (89–95); length of hind foot, 110, 98 (88–105). Body mass of male was 1,175 g. Female mass averaged 969 g (*SD*, 16 g; range, 783–1,075 g). Body mass of 8 captive fennecs (sex unknown) averaged 1,106 g (*SD*, 24 g—Noll-Banholzer 1979a), whereas 7 animals (4 males, 3 females) hand-reared at the Tel Aviv University weighed 1.20 kg (range, 1.15–1.25 kg—Maloiy et al. 1982).

Skull (Fig. 2) is small and delicate with enlarged auditory bullae (Harrison 1968). Rostrum is very delicate, and its width is <50% that of braincase. Zygomatic arches are widely flared anteriorly, so that their midparts are nearly parallel. Postorbital region is wide, and postorbital process is small. Sagittal crest is only detectable as a low elevation in front of lambda, and temporal ridges are small. Mandible is very delicate with a marked convexity to lower border (Harrison 1968).

Canines are slender, and their greatest width is equal to one-third of their height. Anterior upper premolars are widely spaced from each other and from canines. Skull measurements (in mm) of 1 female from Libya are: zygomatic breadth, 45; length of auditory bullae, 22 (Hufnagl 1972). Zygomatic breadth of 1 male from Kuwait is 44 mm (Harrison 1968). Greatest length of skull varies between 80 and 87 mm (Harrison 1968). Skull measurements (in mm) and parenthetical range from 1 male and 3 females born in captivity from North African parents (Mendelssohn and Yom-Tov 1987) are: greatest length of skull, 88.7, 86.1 (83.5–88.1); condylobasal length, 85.9, 83.1 (81.3–84.3); zygomatic breadth, 48.2, 46.8 (46.0–47.5); breadth of braincase, 37.7, 36.7 (36.2–37.2); in-



FIG. 1. Adult *Vulpes zerda*. Photograph from the Mammal Slide Library, American Society of Mammalogists.

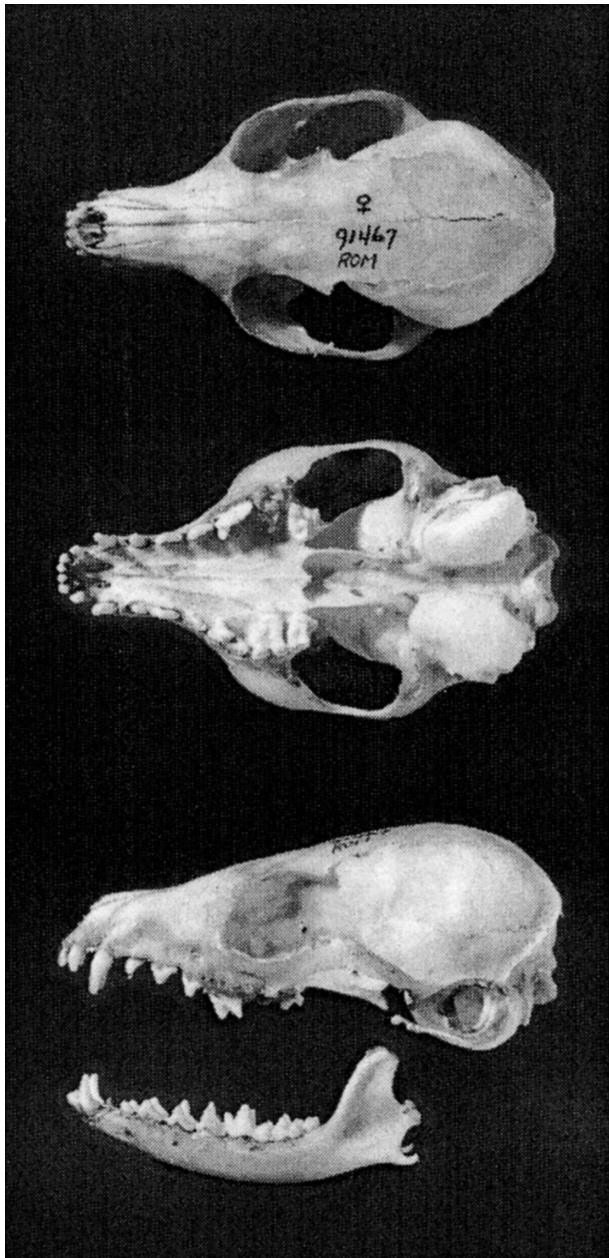


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Vulpes zerda* (female, Royal Ontario Museum, #91467). Greatest length of cranium is 85.1 mm.

terorbital constriction, 16.7, 16.4 (16.0–16.6); length of maxillary tooththrow, 37.7, 36.5 (36.0–37.2); length of mandibular tooththrow, 41.6, 41.0 (40.8–41.0); length of mandible, 64.7, 62.2 (61.8–62.7).

Males have a well-developed baculum that is triangular in cross section. Distal two-thirds is straight, whereas proximal third is angled upward. A well-defined groove is present on entire ventral side (Chaîne 1925). Length and width of 1 baculum were 31 and 3 mm, respectively (Didier 1946).

DISTRIBUTION. The fennec lives in the northernmost tier of African countries, from Morocco through Algeria, Tunisia, Niger, Libya, Egypt, and Sudan (Fig. 3). Only 2 occurrences outside the African continent have been confirmed: 1 in the Sinai and 1 in Kuwait (Nowak 1991). It is rare or occasional in Arabia (Al-Robaae 1982; Harrison 1968; Kingdon 1990), where it is often confused with *V. rueppelli* (Kowalski and Rzebik-Kowalska 1991; Sheldon 1992). Important populations occur in Morocco (Cuzin 1996) and Lybia (Hufnagl 1972). In Algeria, the fennec inhabits sandy regions of the entire Sahara, but it is absent in areas without sand dunes (Kowalski and Rzebik-Kowalska 1991).

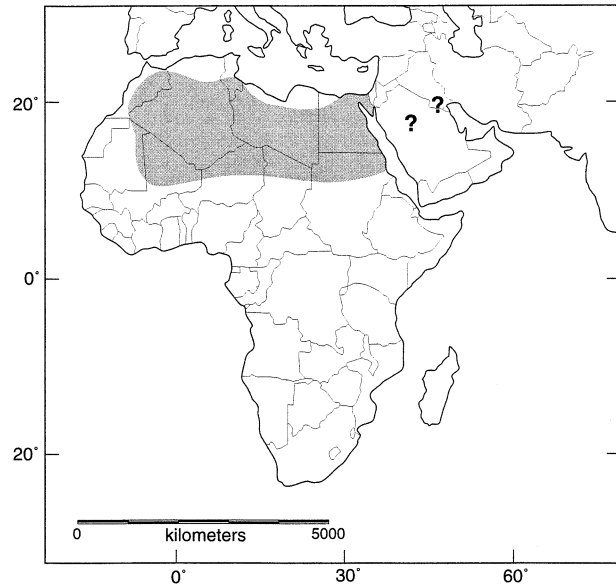


FIG. 3. Distribution of *Vulpes zerda*, modified from Gasperetti et al. (1985), Kingdon (1997), and Kowalski and Rzebik-Kowalska (1991).

FOSSIL RECORD. Canids occur in the Miocene of Africa (Kowalski and Rzebik-Kowalska 1991), and a *Vulpes*-like animal occurred in late Pliocene deposits in Ahl al Oughlam (Morocco—Geraads 1997). *V. zerda* first appeared in the late Pleistocene (Savage 1978).

Time of divergence between *V. zerda* and *V. cana* suggests that a foxlike progenitor entered the Middle East and northern Africa, coinciding with appearance of desert regions, and then diversified into 2 lineages (Geffen et al. 1992b). Desert adaptations evolved independently at least twice in the Canidae, once in the form of *V. zerda* and *V. cana*, and more recently in the form of *V. velox* and *V. rueppelli* (Geffen et al. 1992b).

FORM AND FUNCTION. *Vulpes zerda* has numerous adaptations to life in the desert. Soles of the feet are covered by long, soft hairs that conceal the pads completely, an adaptation to extreme temperatures (Sheldon 1992) and to facilitate locomotion in loose sand (Bekoff 1975). Sandy color of pelage camouflages the fennec in desert environments (Gauthier-Pilters 1967). Thick coat provides thermoregulatory advantages during cold desert nights (Sheldon 1992). Large ears and a hypertrophy of bullae give fennecs excellent hearing, enabling detection of burrowing insects and small mammals (Gauthier-Pilters 1967).

In captivity, fennecs exhibit a circadian cycle of body temperature and heart rate. Both values decrease in midday and increase at night as animals become active. Body temperature of resting animals is ca. 37.5°C, whereas heart rate is ca. 100–115 beats/min (Maloiy et al. 1982; Noll-Banholzer 1979a). Thermoneutral zone of fennecs ranges from 23 to 37°C (Maloiy et al. 1982; Noll-Banholzer 1979a). Panting occurs when temperatures exceed 37°C (Maloiy et al. 1982). Thermoregulatory mechanisms include vasodilation under heat stress and vasoconstriction under cold conditions. Resting postures vary with ambient temperature: under cold stress (10–20°C), piloerection and shivering were observed (Maloiy et al. 1982). Basal metabolic rate is 0.358 ml/g h and is 39% lower than that predicted by body mass (Noll-Banholzer 1979a). Newborn fennecs are sensitive to cold but are incapable of thermoregulation.

Vulpes zerda drinks freely when water is available but may subsist without water for an indefinite period (Noll-Banholzer 1979b). Instead, fennecs depend on their nocturnal activity patterns, use of burrows during the day, and moisture content of their prey. Most water loss in fennecs is due to urine, and reduction in water intake leads to reduction to urinary water. Kidneys of the fennec filter extremely high concentrations of urea with little water loss (Noll-Banholzer 1979b). Evapotranspiration varies little with water intake. Under heat stress, fennecs deprived of water decrease their activity and food intake and consequently lose weight. Thus,

high ambient temperatures are more critical to the subsistence of fennecs than the lack of water (Noll-Banholzer 1979b).

Skeleton of *V. zerda* comprises slender bones (Hildebrand 1954). Praesacral spine contains 27 vertebrae (7 C, 13 T, 7 L). Lumbar peak of praesacral spine is higher than that of cervical spine (Herán 1996). Ratio of cervical:thoracal:lumbal weight of spine segments is 1.14:1:1.18 (Herán 1996).

Dentition is weak (Harrison 1968). Canines are small, slender, and sharp (Dayan et al. 1989; Harrison 1968). Dental formula is $i\ 3/3, c\ 1/1, p\ 4/4, m\ 2/3$, total 42.

Adrenal gland of the fennec is rostral to anterior pole of kidney. Adrenal glands are encapsulated within fibrous connective tissue that contains nerve fibers, ganglion cells, and large veins. Numerous arterioles are also located within capsules (El-Desouki 1996). Carbohydrates, acid mucopolysaccharides, and proteins are present in large amounts in adrenal cortex of *V. zerda* (El-Desouki 1996). Cortical cells are characterized by a prominent nucleolus, elongated mitochondria, and a concave Golgi apparatus (El-Desouki 1996).

ONTOGENY AND REPRODUCTION. Fennecs usually have 1 litter per year, but if the 1st one is lost, a 2nd, and sometimes a 3rd litter may be produced (Koenig 1962). Thus, females are not truly monestrous as no anestrus period occurs between end of pseudopregnancy and subsequent proestrus, or between end of lactation and next proestrus (Asa and Valdespino 1998).

Testicular recrudescence in males is synchronized with the cycle of females. Testis volume and sperm output vary during the year. Both are elevated when females are in estrus (Asa and Valdespino 1998). In addition, testis activity declines following mating.

Estrus lasts 1–2 days (Gauthier-Pilters 1967), and proestrus, based on vulval swelling, is brief. In captivity, breeding occurs mostly February–April (Gangloff 1972; Saint Girons 1962) but may occur in summer or autumn (Dulaney 1981; Weiher 1976). Parturition occurs February–June (Dulaney 1981; Gauthier-Pilters 1967; Petter 1957; Rensch 1950; Volf 1957) after a gestation of 50–51 days (Petter 1957; Saint Girons 1962; Sowards 1981; Volf 1957). Litter size is usually 2–5 but varies from 1 to 6 (Dorst and Dandelot 1970; Gangloff 1972; Koenig 1962; Saint Girons 1962).

Young are born blind and fully furred (Petter 1952; Saint Girons 1962). Measurements (in mm) of three 1-day-old pups are: length of head and body, 108, 109, 115; length of tail, 45, 46, 46; length of ear, 10, 10, 11 (Petter 1952; Weiher 1976); body masses of two 1-day-old cubs are: 40.0 and 44.5 g (Weiher 1976). Cubs double their body mass after 11–12 days (Weiher 1976). Body mass (g) of 5 cubs at 51 days of age are: 200, 430 for 2 males, and 330, 330, 405 for 3 females (Gangloff 1972).

Eye opening occurs after 8–11 days (Gangloff 1972; Weiher 1976), and cubs become mobile after 14 days (Gangloff 1972). Upper canines erupt after 13 days, and lower canines and incisors erupt after 15 days (Weiher 1976). Young first eat meat at 3 weeks of age, but weaning occurs at 61–70 days (Koenig 1962). Young fennecs are easily tamed if captured before 3 weeks of age (Gauthier-Pilters 1967; Vogel 1962). Primitive hunting behavior appears during the 7th week (Gauthier-Pilters 1962). Offspring reach adult size and sexual maturity at 9–11 months of age (Koenig 1962).

ECOLOGY. Fennecs require a soft substrate for burrowing and thus are found mainly in sand dunes (Dorst and Dandelot 1970; Sheldon 1992). Fennecs mostly feed on grasshoppers and locusts but also eat other insects (including those that secrete noxious fluids), rodents, birds, lizards, and roots (Dorst and Dandelot 1970; Kingdon 1990). Parasites include trematodes (*Alaria alata*, *Joyeuxiella echinorhyncoides*, *Tania crassiceps*) and nematodes (*Ancylostoma braziliense*, *A. caninum*, *A. duodenale*, *Cyathospirura seurati*, *Oxyntema crassispiculum*, *Physaloptera cestitellata*, *Rictularia cahirensis*, *Spirocerca lupi*, *Spirura rytiplerites*, *Streptopharagus numidicus*, *Toxascaris*, *Toxocara musculi*, *Uncinaria stenocephala*)—Round 1968; Sood and Toong 1973).

Because of its specialized form and highly restricted habitat, *V. zerda* is not a potential competitor of the red fox and probably not an important competitor of the Rueppell's sand fox (Dayan et al. 1989). Domestic cats may compete with fennecs in some areas (Kingdon 1990). The fennec is not sympatric with Blanford's fox (*Vulpes cana*)—Dayan et al. 1989).

Fennecs may be killed by domestic dogs, jackals, and hyenas. Intraspecific strife may also result in death of old males during the

breeding season (Koenig 1962). However, dogs and humans are probably the most serious threat to fennecs today (Kingdon 1990). Fennecs are hunted intensively by humans in the Sahara region, with resultant population declines in some parts of northwestern Africa. Longevity of captive animals may reach almost 13 years (Dobroruka 1967; Flower 1931; Saint Girons 1971).

BEHAVIOR. The basic social unit of *V. zerda* is a monogamous pair and their offspring. Offspring from the previous year may remain with the family group (Gauthier-Pilters 1967), and groups of up to 10 individuals may occur (Dorst and Dandelot 1970).

Affiliative behaviors include tail-wagging, greeting displays, other facial expressions, squeaking, ducked posture, and rolling over. Displays can be directed toward conspecifics or familiar human keepers (Gauthier-Pilters 1962, 1966, 1967). Quarrels may occur over food or following intense play (Gauthier-Pilters 1967).

The fennec has a wide variety of calls including soft barks used as warning calls, high-pitched barks, catlike purring when pleased, yapping as threats, or squeaking as greeting (Gauthier-Pilters 1967; Harrison 1968). In the wild, a rutting cry may be emitted when a pair is separated (Gauthier-Pilters 1967).

In captivity, typical courting behavior includes romping and playing (Sowards 1981). Courtship lasts for 24–36 h (Koenig 1962). Copulation lasts 75 min and may occur several times at 2–3 h intervals (Gauthier-Pilters 1967). Fennecs do not always adopt the coital lock (Dulaney 1981; Petter 1952; Sowards 1981). In captivity, both males and females may accept offspring as sexual partners (Koenig 1962).

During the breeding season, males become more aggressive and frequently mark objects with urine (Gauthier-Pilters 1962). In captivity, males defend females before and during parturition. After parturition, the male defends the nest box but never enters it (Koenig 1962). Males provide food and defend the den and den area until pups are 4 weeks old (Gauthier-Pilters 1962, 1966, 1967; Koenig 1962; Sowards 1981). In captivity, active defense of the young decreases with age of pups and disappears after 4 weeks (Koenig 1962).

For successful breeding in captivity, females must be allowed uninterrupted visual, auditory, and olfactory contact with conspecifics, possibly indicating the social nature of fennecs (Gangloff 1972). Females are most sensitive to disturbance immediately after parturition. Security of the nest box is very important (Koenig 1962). Suckling occurs initially inside the nest box, then after day 19, young are suckled outside (Koenig 1962). Carrying of prey to young occurs between weeks 1 and 13 and is most intensive when young are between 4 and 10 weeks of age (Koenig 1962). Grooming of young and suckling activity follow similar intensity (Koenig 1962). From day 20 onward, cubs may sunbath (Koenig 1962). Females transport young by grasping them by the neck (Gauthier-Pilters 1967), and transport of young may serve as a stress-release mechanism when the female is restless. Young offspring wriggle in the mother's mouth, whereas older juveniles exhibit carriage lethargy (Koenig 1962).

The fennec is mainly nocturnal (Gauthier-Pilters 1967), but some crepuscular activity may occur (Dorst and Dandelot 1970). During the day, fennecs shelter in burrows excavated in the sand (Gauthier-Pilters 1967). Burrows can also be used to escape predators (Kingdon 1990).

The fennec digs its own burrows, which may reach up to 10 m in length and 1 m in depth. Burrows are dug in low areas where moisture concentrates, and several dens may be interconnected or located close together (Gauthier-Pilters 1967). Fennecs are rapid diggers, and pups can dig a 40-cm burrow in <10 min (Gauthier-Pilters 1967). While digging, fennecs throw sand between their back legs. To enlarge burrows, fennecs lie on their side, prop their back legs against the sidewalls, and dig with their front paws (Gauthier-Pilters 1967).

Fennecs hunt alone. Prey are located primarily by sound, and prey hidden in the sand are excavated by digging with all 4 feet (Kingdon 1990). Most prey are killed by a bite to the neck. Fennecs are capable of killing prey larger than themselves, including full-grown rabbits (Gauthier-Pilters 1962). Heads of mammalian prey are eaten first, and birds are eaten with the feathers. Extra food may be cached for later use (Gauthier-Pilters 1967). Food caching occurs in a way similar to that of *V. vulpes*: a hole is dug, food is deposited, and sand is pushed over the food with the nose (Gau-

thier-Pilters 1967). Females cache more frequently than males (Gauthier-Pilters 1962).

Play is common in pups, juveniles, and adults and involves either object-oriented or conspecific-oriented play. Males are less playful during the breeding season and show high levels of aggression. Play with food is common in juveniles (Gauthier-Pilters 1962, 1966, 1967).

Males may urine-mark objects and do so more during the breeding season (Gauthier-Pilters 1962). Captive fennecs also exhibit site-specific defecation. Feces are deposited in a shallow depression scraped with their feet and subsequently covered by pushing dirt over the depression with the nose or by rapidly scraping with the hind feet (Gauthier-Pilters 1962).

GENETICS. The fennec has $2n = 64$ chromosomes. The X chromosome is a large submetacentric, and the Y chromosome is very small. The autosomal complement consists of 29 pairs of acrocentrics and 2 pairs of metacentric and submetacentric chromosomes (Matthey 1954; Würster and Benirschke 1968). A receptor gene of *V. zerda* has been used in comparative analyses of olfaction (Issel-Tarver and Rine 1997).

CONSERVATION STATUS. *Vulpes zerda* is listed on the Appendix II of the Convention for the International Trade of Endangered Species and is listed as insufficiently known by the International Union for the Conservation of Nature (Nowak 1991; Wozencraft 1993).

REMARKS. Meyer 1793:91 as cited by Kowalski and RzebiK-Kowalska (1991) does not mention the fennec. References to the fennec in Arabia often confuse *V. rueppelli* and *V. zerda* (Harrison 1968). The generic name *Vulpes* is Latin for fox, whereas the specific epithet *zerda* is from the Greek meaning cunning (Borror 1960).

D. Dyck and M. Mierau helped with the map. S. Woodward kindly provided photographs of the skull. L. R. Walton reviewed an earlier draft of the manuscript.

LITERATURE CITED

- AL-ROBAAE, K. 1982. Northeast extension of the geographic distribution of fennec fox *Fennecus zerda* Zimmerman in the Arabian peninsula. Bulletin of the Basrah Natural History Museum 5:61–64.
- ASA, C. S., AND C. VALDESPINO. 1998. Canid reproductive biology: an integration of proximate mechanisms and ultimate causes. American Zoologist 38:251–259.
- BEKOFF, M. 1975. Social behavior and ecology of the African Canidae: a review. Pp. 120–142 in The wild canids: their systematics, behavioral ecology and evolution (M. W. Fox, ed.). Robert E. Krieger Publishing Company, Malabar, Florida.
- BOITARD, M. 1842. Le jardin des plantes: description et moeurs des mammifères de la ménagerie et du muséum d'histoire naturelle. J.-J. Dubochet, Paris, France.
- BORROR, D. J. 1960. Dictionary of word roots and combining forms. National Press Books, Palo Alto, California.
- CHAÏNE, J. 1925. Les pénien: étude descriptive et comparative. Actes de la Société Linnéenne de Bordeaux 78:5–195.
- CLUTTON-BROCK, J., G. B. CORBET, AND M. HILLS. 1976. A review of the family Canidae, with a classification by numerical methods. British Museum of Natural History 29:117–199.
- CORBET, G. B. 1978. The mammals of the Palaearctic region, a taxonomic review. British Museum of Natural History and Cornell University Press, London, United Kingdom.
- CUZIN, F. 1996. Répartition actuelle et statut des grands mammifères sauvages du Maroc (Primates, Carnivores, Artiodactyles). Mammalia 60:101–124.
- DAYAN, T., E. TCHERNOV, Y. YOM-TOV, AND D. SIMBERLOFF. 1989. Ecological character displacement in Saharo-Arabian Vulpes: outfoxing Bergmann's rule. Oikos 55:263–272.
- DESMAREST, A. G. 1804. Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, principalement à l'agriculture et à l'économie rurale et domestique: par une société de naturalistes et d'agriculteurs: avec des figures tirées des trois règnes de la nature. Deterville, Paris, France 24:1–238.
- DESMAREST, A. G. 1820. Mammalogie ou description des espèces de mammifères. Encyclopédie méthodique. Veuve Agasse, Paris, France.
- DIDIER, R. 1946. Étude systématique de l'os pénien des mammifères. Mammalia 10:78–91.
- DOBRORUKA, L. J. 1967. La durée de vie de quelques mammifères du Parc Zoologique de Prague. Mammalia 31:515–517.
- DORST, J., AND P. DANDELLOT. 1970. A field guide to the larger mammals of Africa. Houghton Mifflin Company, Boston, Massachusetts.
- DULANEY, M. 1981. Successful birth and rearing of fennec foxes at the Cincinnati Zoo. Animal Keepers' Forum 8:147–148.
- EL-DESOUKI, N. I. 1996. Histological, histochemical and fine structural studies on the adrenal cortex of the carnivore fennec, *Vulpes zerda* and herbivore rabbits, *Oryctolagus cuniculus*. Journal of the Medical Research Institute 17:122–141.
- ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1966. Checklist of Palearctic and Indian mammals. Second edition. Pp. 1758–1946. British Museum of Natural History, London, United Kingdom.
- FLOWER, S. S. 1931. Contributions to our knowledge of the duration of life in vertebrate animals. Proceedings of the Zoological Society of London 1931:145–234.
- GANGLOFF, L. 1972. Breeding fennec foxes *Fennecus zerda* at Strasbourg Zoo. International Zoo Yearbook 12:115–116.
- GASPERETTI, J., D. L. HARRISON, AND W. BUTTIKER. 1985. The carnivora of Arabia. Fauna of Saudi Arabia 7:397–413.
- GAUTHIER-PILTERS, H. 1962. Beobachtungen an feneks (*Fennecus zerda* Zimm.). Zeitschrift für Tierpsychologie 19:440–464.
- GAUTHIER-PILTERS, H. 1966. Einige beobachtungen über das Spielverhalten beim fenek (*Fennecus zerda* Zimm.). Zeitschrift für Tierpsychologie 31:337–350.
- GAUTHIER-PILTERS, H. 1967. The fennec. African Wild Life 21: 117–125.
- GEFFEN, E., R. HEFNER, D. W. MACDONALD, AND M. UCKO. 1992a. Morphological adaptations and seasonal weight changes in Blanford's fox, *Vulpes cana*. Journal of Arid Environments 23: 287–292.
- GEFFEN, E., A. MERCURE, D. J. GIRMAN, D. W. MACDONALD, AND R. K. WAYNE. 1992b. Phylogenetic relationships of the fox-like canids: mitochondrial DNA restriction fragment, site and cytochrome b sequence analysis. Journal of Zoology, London 228:27–39.
- GERAADS, D. 1997. Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). Geobios 30:127–164.
- GMELIN, J. F. 1788. Revision of "Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis, locis" by C. Linnaeus. G. E. Beir, Lipsiae, Germany 1:1–232.
- GRAY, J. E. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum of Natural History, London, United Kingdom.
- HARRISON, D. L. 1968. The mammals of Arabia: Carnivora, Artiodactyla, Hyracoidea. Ernest Benn Limited, London, United Kingdom 2:1–381.
- HERÁN, I. 1996. Interspecific difference in proportions of the praesacral spine in Canidae (Mammalia: Carnivora). Acta Societatis Zoologicae Bohemoslovenicae 60:31–36.
- HILDEBRAND, M. 1954. Comparative morphology of the body skeleton in recent Canidae. University of California Press, Berkeley.
- HUFNAGL, E. 1972. Lybian mammals. The Olander Press, New York.
- ILLIGER, J. K. W. 1811. Prodomus systematis mammalium et avium. Sumptibus C. Salfeld, Berlin, Germany.
- ISSEL-TARVER, L., AND J. RINE. 1997. The evolution of mammalian olfactory receptor genes. Genetics 145:185–195.
- KINGDON, J. 1990. Arabian mammals: a natural history. Academic Press, London, United Kingdom.
- KINGDON, J. 1997. The Kingdon field guide to African mammals. Academic Press, San Diego, California.
- KOENIG, L. 1962. Zur fortpflanzung und jugendentwicklung des wüstenfuchses (*Fennecus zerda* Zimm. 1780). Zeitschrift für Tierpsychologie 27:205–246.
- KOWALSKI, K., AND B. RZEBIK-KOWALSKA. 1991. Mammals of Algeria. Polish Academy of Sciences, Institute of Systematics and evolution of Mammals, Krakow, Poland.
- LESSON, R.-P. 1827. Manuel de mammalogie ou histoire naturelle des mammifères. Roret, Paris, France.

- MALOY, G. M. O., J. M. Z. KAMAU, A. SHKOLNIK, M. MEIR, AND R. ARIELI. 1982. Thermoregulation and metabolism in a small desert carnivore: the fennec fox (*Fennecus zerda*) (Mammalia). *Journal of Zoology*, London 198:279–291.
- MATTHEY, R. 1954. Chromosomes et systématique des canidés. *Mammalia* 18:225–230.
- MENDELSSOHN, H., AND Y. YOM-TOV. 1987. Plants and animals of the land of Israel: an illustrated encyclopedia: mammals. Ministry of Defence, The Publishing House, Society for Protection of Nature, Tel Aviv, Israel 7:1–295.
- MEYER, F. A. A. 1793. Systematisch-summarische Uebersicht der neuesten zoologischen Entdeckungen in Neuholland und Africa. *Zoologische Annalen* (Weimar) 1:xxvi–412.
- NOLL-BANHOLZER, U. 1979a. Body temperature, oxygen consumption, evaporative water loss and heart rate in the fennec. *Comparative Biochemistry and Physiology, A. Comparative Physiology* 62:585–592.
- NOLL-BANHOLZER, U. 1979b. Water balance and kidney structure in the fennec. *Comparative Biochemistry and Physiology, A. Comparative Physiology* 62:593–597.
- NOWAK, R. M. 1991. Walker's mammals of the world. Fifth edition. John Hopkins University Press, Baltimore, Maryland 2: 1–1629.
- PETTER, F. 1952. Le ranard famélique. *Terre et Vie* 152:190–193.
- PETTER, F. 1957. La reproduction du fennec. *Mammalia* 21:307–309.
- RENSCH, B. 1950. Beobachtungen an einen fenek, *Megalotis zerda* Zimm. *Der Zoologische Garten* 17:30–40.
- ROUND, M. C. 1968. Check list of the helminth parasites of African mammals of the orders Carnivora, Tubulidentata, Proboscidea, Hyracoidea, Artiodactyla and Perissodactyla. Technical Communication on the Commonwealth Bureau of Helminthology, St. Albans 38:1–252.
- SAINT GIRONS, M. C. 1962. Notes sur les dates de reproduction en captivité du fennec, *Fennecus zerda* (Zimmerman 1780). *Zeitschrift für Säugetierkunde* 27:181–184.
- SAINT GIRONS, M. C. 1971. Durée de vie du fennec en captivité. *Mammalia* 35:666–667.
- SAVAGE, R. J. G. 1978. Carnivora. Pp. 249–267 in *Evolution of African mammals* (V. J. Maglio and H. B. S. Cooke, eds.). Harvard University Press, Cambridge, Massachusetts.
- SHELDON, J. W. 1992. Wild dogs: the natural history of the non-domestic Canidae. Academic Press, New York.
- SOOD, M. L., AND R. TOONG. 1973. *Streptopharagus guptai* n. sp. (Nematoda: Spiruridae) from the rectum of a rhesus macaque *Macaca mulatta* from India. *Zoologischer Anzeiger* (Leipzig) 190:132–136.
- SOWARDS, R. K. 1981. Observations on breeding and rearing the fennec fox (*Fennecus zerda*) in captivity. *Animal Keepers' Forum* 8:175–177.
- TEDFORD, R. H., B. E. TAYLOR, AND X. WANG. 1995. Phylogeny of the Canidae (Carnivora: Canidae): the living taxa. *American Museum Novitates* 3146:1–37.
- VAN GELDER, R. G. 1978. A review of canid classification. *American Museum Novitates* 2646:1–10.
- VOLF, J. 1957. A propos de la reproduction du fennec. *Mammalia* 21:454–455.
- WAYNE, R. K., E. GEFFEN, D. J. GIRMAN, K. P. KOEFLI, L. M. LAU, AND C. R. MARSHALL. 1997. Molecular systematics of the Canidae. *Systematic Biology* 46:622–653.
- WEIHER, E. 1976. Hand-rearing fennec foxes *Fennecus zerda* at Melbourne Zoo. *International Zoo Yearbook* 16:200–202.
- WOZENCRAFT, W. C. 1993. Order Carnivora. Pp. 279–348 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.
- WURSTER, D. H., AND K. BENIRSCHKE. 1968. Comparative cytogenetic studies in the Order Carnivora. *Chromosoma* 24:336–382.
- ZIMMERMAN, E. A. W. 1780. *Geographische Geschichte des Menschen, und der vierfüßigen Thiere*. Weygandschen Buchhandlung, Leipzig, Germany 2:1–432.

Associate editors of this account were ELAINE ANDERSON and VIRGINIA HAYSEN. Editor was VIRGINIA HAYSEN.

S. LARIVIÈRE, DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATCHEWAN, 112 SCIENCE PLACE, SASKATOON, SASKATCHEWAN S7N 5E2, CANADA AND DELTA WATERFOWL FOUNDATION, R.R. #1, BOX 1, PORTAGE LA PRAIRIE, MANITOBA R1N 3A1, CANADA.