

Atelerix albiventris (Erinaceomorpha: Erinaceidae)

ERICA M. SANTANA, HOLLY E. JANTZ, AND TROY L. BEST

School of Forestry and Wildlife Sciences, 3301 Forestry and Wildlife Science Building, Auburn University, AL 36849, USA; ems0005@auburn.edu (EMS); jantzhe@auburn.edu (HEJ)

Department of Biological Sciences and Alabama Agricultural Experiment Station, 331 Funchess Hall, Auburn University, AL 36849-5414, USA; besttro@auburn.edu (TLB)

Abstract: *Atelerix albiventris* (Wagner, 1841) is an erinacid with variable common names but is most widely known as the four-toed hedgehog. One of 4 members of the genus *Atelerix*, *A. albiventris* is the smallest of the African hedgehogs. These nocturnal insectivores are sexually dimorphic and widespread, and are not a species of special conservation concern. Native to equatorial Africa, they inhabit steppes, savannas, grasslands, and agricultural fields. *A. albiventris* has been domesticated and is widely used in biomedical research and sold in the exotic pet trade. DOI: 10.1644/857.1.

Key words: Africa, erinacid, erinaceomorph, hedgehog, insectivore, orbicularis panniculi, sexually dimorphic

© 26 May 2010 American Society of Mammalogists
Synonymies completed 17 December 2009

www.mammalogy.org



Atelerix Pomel, 1848

Erinaceus: Wagner, 1841:14, 22. Part.

Atelerix Pomel, 1848:251. Type species *Erinaceus 4 dactylus* (= *quadridactylus*) Pomel, 1848, by monotypy; described as a subgenus of *Erinaceus* Linnaeus, 1758.

Peroëchinus Fitzinger, 1866:565. Type species *Erinaceus pruneri* Wagner, 1841, by original designation.

Æthechinus O. Thomas, 1918a:194. Type species *Erinaceus algirus* Lereboullet, 1842, by original designation.

CONTEXT AND CONTENT. Order Erinaceomorpha, family Erinaceidae, subfamily Erinaceinae. The genus *Atelerix* currently contains 4 species (Hutterer 2005): *A. albiventris* (Wagner, 1841), *A. algirus* (Lereboullet, 1842), *A. frontalis* A. Smith, 1831, and *A. sclateri* Anderson, 1895. A key to species follows (modified from Frost et al. 1991):

1. P3 lingual lobe vestigial or absent 2
P3 lingual lobe present 3
2. Maxilla does not share common suture with nasals *A. sclateri*
Maxilla shares common suture with nasals ... *A. albiventris*
3. P2 with 1 or 2 roots *A. algirus*
P2 with 3 roots *A. frontalis*

Atelerix albiventris (Wagner, 1841) Four-toed Hedgehog

E[rinaceus]. albiventris Wagner, 1841:14, 22. Type locality unknown; stated as “in all probability, from Senegam-

bia” by Anderson and de Winton (1902:164), “Northern African—Senegal to Egypt, southwards to British East Africa” by Thomas (1918a:195), and “probably Senegal or Gambia” by Hutterer (2005:212).

E[rinaceus] pruneri Wagner, 1841:23. Type locality “Upper Nile, taken at Sennaar, where Pruner travelled” vide Setzer (1956:454).

Erinaceus heterodactylus Sundevall, 1842:227. Type locality “Bahr-el-Abiad, Sennaar.”



Fig. 1.—Adult male *Atelerix albiventris* from Mount Kasigau, Coast Province, Kenya; note the prominent spines on the dorsum. Used with permission of the photographer Charles H. Kilgore.

- Erinaceus diadematus* Fitzinger, 1867:853. Type locality “Sennaar und Kordofán.”
- Erinaceus adansoni* de Rochebrune, 1883:7. Type locality “Saint-Louis, Pointe de Barbarie, Cap Vert, Joalles, etc.”
- Erinaceus albiventris atratus* Rhoads, 1896:544. Type locality “Ngare Nochor, Lake Rudolf, Africa.”
- Erinaceus hindei* O. Thomas, 1910:193. Type locality “Kitui, British East Africa. Alt. 3500’.”
- Erinaceus sotika* Heller, 1910:1. Type locality “Guaso Nyiro River, Sotik District, British East Africa.”
- Atelerix albiventris*: O. Thomas, 1918a:195. First use of current name combination.
- Atelerix spinifex* O. Thomas, 1918b:231. Type locality “Illela, 95 miles north of Sokoto, Nigeria.”
- Atelerix kilimanus* O. Thomas, 1918b:232. Type locality “Kilima-njaro. Rombo, alt. 5300’.”
- Atelerix faradjius* J. A. Allen, 1922:13. Type locality “Faradje, northeastern Belgian Congo.”
- Atelerix langi* J. A. Allen, 1922:15. Type locality “Faradje, northeastern Belgian Congo.”
- Erinaceus spiculus* Thomas and Wroughton, 1907:371. Type locality “Maifoni, near Lake Chad” [Nigeria vide Hutterer 2005:212].
- Erinaceus (Atelerix) pruneri oweni* Setzer, 1953:237. Type locality “Torit, 2,000 feet, Equatoria Province, Anglo-Egyptian Sudan.”
- Atelerix pruneri lowei* Setzer, 1956:453. Type locality “Umm Keddada, Darfur Province, Anglo-Egyptian Sudan.”

CONTENT AND CONTEXT. Context as for genus. No convincing arrangement of subspecies has been proposed for *Atelerix albiventris* (Hutterer 2005). *A. albiventris* is referred to as hérisson à ventre blanc in French.

DIAGNOSIS

Atelerix albiventris (Fig. 1) differs from all other species in the genus *Atelerix* by lacking a hallux (Kingdon 1974) and by a maxilla that shares a common suture with the nasals (Frost et al. 1991; Fig. 2). The North African hedgehog (*A. algirus*) and southern African hedgehog (*A. frontalis*) have a normal 3rd upper premolar and are larger in body size than *A. albiventris* (condylobasal length in *A. algirus* and *A. frontalis* is 45–55 mm). *A. frontalis* has darker legs and undersides, and *A. algirus* has longer ears than *A. albiventris* (length of ear in *A. algirus* > 25 mm—Haltenorth and Diller 1988). All species of *Atelerix* have a band of white fur across the forehead (Reeve 1994).

GENERAL CHARACTERS

Atelerix albiventris is a small, short-tailed, spiny erinaceomorph with a pointed muzzle, short, hairy legs,



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of adult female *Atelerix albiventris* from 12 miles N Sokoto, Nigeria (United States National Museum of Natural History 378743). Greatest length of skull is 38.2 mm. Used with permission of the photographer Donald Hurlburt.



Fig. 3.—Ventral view of a male *Atelerix albiventris* from Mount Kasigau, Coast Province, Kenya, illustrating lack of spines on the venter and showing the external penis located in the middle of the abdomen. Used with permission of the photographer Troy L. Best.

and clawed, well-padded toes (Kingdon 1997) that are short and close together (Catania et al. 2000). *A. albiventris* has a generalized body plan (Kingdon 1974), with masses of 250–600 g (Smith 1992) but typically about 335 g (Symonds 1999). Average measurements (mm) were: length of head and body, 210; length of tail, 25; length of hind foot, 30; and length of ear, 25 (Happold 1987).

Atelerix albiventris has black eyes and large dark ears (Happold 1987). The body is speckled black and white with no dorsal stripe (Haltcnorth and Diller 1988). The muzzle is brown, and the face, legs, and ventral surface are covered with white hair (Happold 1987). Longer hair from the forehead extends forward in a narrow line from eye level to halfway to the tip of the nose and continues ventrally with a narrow strip of minute gray hairs extending to the mustachial vibrissae, cutting off on each side of the eye (Allen 1922). The snout has macrovibrissae on the lateral surface (Brecht et al. 1997), and there are microvibrissae on the tip of the snout, slightly below the glabrous surface of the skin (Catania 2005). The tail is a thinly haired, short stump, and the feet are dark and lightly covered with hair (Happold 1987).

Atelerix albiventris has spines without barbs that are 0.5–1.0 cm in length, located on the dorsal surface, on top of a layer of areolar fat and subcutaneous tissue (Smith 1992). The entire body, except the cranial–caudal tract (2 cm long by 0.5 cm wide), is covered dorsally with short spines (Fairly et al. 1999; Herter 1965); the longest spine on the body is

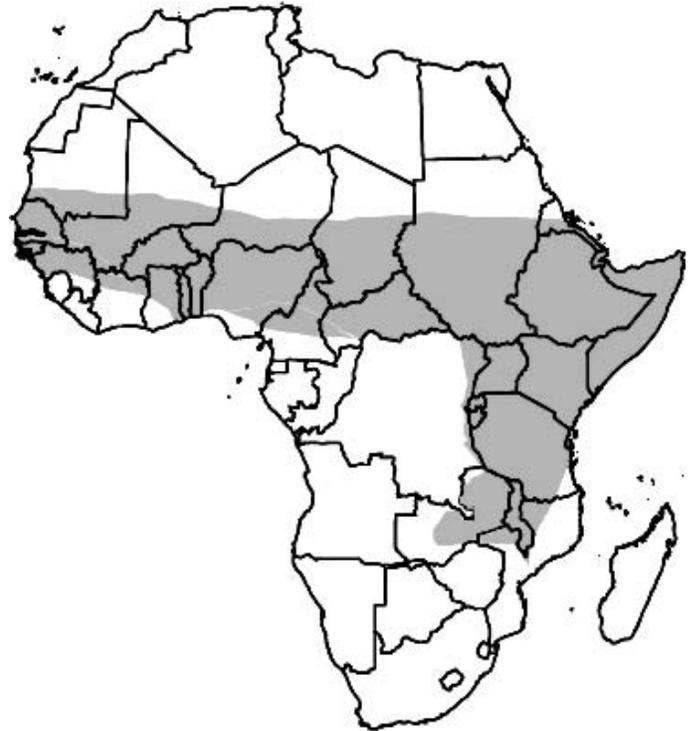


Fig. 4.—Distribution of *Atelerix albiventris* in central and eastern Africa (modified from www.gisbau.uniroma1.it/data/amd/amd255/amd255.pdf).

about 15 mm, and the longest spine on the head is about 17 mm (Allen 1922). Spines on the head are not medially divided (Haltcnorth and Diller 1988). Spines are white at the base and tips with a central band that varies in width and color based on geography (Fairly et al. 1999). Males have numerous elongated white spines that usually are absent in females (Herter 1965), and there are no spines on the venter of *A. albiventris* (Fig. 3).

DISTRIBUTION

Atelerix albiventris is widely encountered in savanna and steppe zones of equatorial Africa from Senegal across to Ethiopia and south to the Zambezi River (Hutterer 2005; Fig. 4). It is uniformly distributed in the Masai Steppe in Tanzania (Kingdon 1974), but rare in other areas of apparently suitable habitat (Easton 1979). It probably occurs throughout Malawi and is common in the Lilongwe, Blantyre, and Mulanje areas, but it is not encountered often elsewhere (Ansell and Dowsett 1988). It is largely widespread but sporadic in drier regions of Africa (Kingdon 1974). The *International Union for Conservation of Nature and Natural Resources Red List of Threatened Species* (Hutterer 2008) lists *A. albiventris* as native to the countries of Benin, Burkina Faso, Cameroon, Central African

Republic, Chad, Côte d'Ivoire, Ethiopia, Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Malawi, Mali, Mauritania, Mozambique, Niger, Nigeria, Senegal, Sierra Leone, Somalia, Sudan, Tanzania, United Republic of Togo, and Uganda, and it is believed to occur in Burundi and Rwanda (Fig. 4).

FOSSIL RECORD

Recent phylogenetic analyses of fossil and extant data indicate that the Erinaceidae group may extend to the Late Cretaceous period (Gould 1995). Erinaceidae was more widespread in Africa during the Miocene and contained nearly 40 extinct forms in the superfamily Erinaceodea (Butler 1969). Six species belonging to 4 genera have been found in East African Miocene deposits (Butler 1969). *Atelerix algirus* has been identified in a Bronze Age gravesite on the island of Minorca (Morales and Rofes 2008). No fossil of *A. albiventris* is known.

FORM AND FUNCTION

Form.—Spines of *Atelerix albiventris* are poorly vascularized and are surrounded by subcutaneous fat, which may account for $\leq 50\%$ of body mass (Smith 1992). Young are born without integumental spines, but they develop within 24 h (Meritt 1981).

Atelerix albiventris has a small skull (condylobasal length < 45 mm; Fig. 2) with a broad posterior palatal shelf; the postglenoid process is smaller than the mastoid process. A zygomatic arch is present (Happold 1987). It has a double-rooted I3 and C3. Third upper premolar is either absent or reduced (Robbins and Setzer 1985). The dental formula is $i\ 3/2$, $c\ 1/1$, $p\ 3/2$, $m\ 3/3$, total 36 (Haltenorth and Diller 1988). Molar teeth are blunt and broad (Kingdon 1974). Measurements (mm) of a preserved female (Allen 1922) were: total length, 249.0; length of head and body, 230.0; length of tail, 19.0; length of hind foot, 29.0; length of ear, 30.0; condyloincisive length, 45.1; length of nasals, 16.5; palatal length (to front of premaxillae), 25.4; zygomatic breadth, 27.7; interorbital breadth, 11.8; breadth of braincase, 19.5; postglenoid breadth, 22.0; mastoid breadth, 15.5; palatal breadth (outside to outside of M1), 17.6; breadth of rostrum at base of front incisor, 6.0; breadth of palate at ridge behind M3, 9.7; tip to tip of alisphenoid processes, 11.2; tip to tip of pterygoids, 6.1; length of mesopterygoid fossa, 10.7; breadth between pterygoids, 2.8; length of upper toothrow (I1–M3), 21.5; length of upper molars, 8.1; length of lower toothrow (to tip of I1), 9.7; length of lower molars, 9.9; length of mandible (front of symphysis to posterior border of condyle), 34.5; and depth of angle to coronoid, 17.7.

Males have a long, smooth, external penis located in the middle of the abdomen (Fig. 3; Bedford et al. 2000; Smith

1992). The glans is fairly flat compared to that of other species in the genus (Bedford et al. 2000). Testicles are in the lower abdomen in para-anal recesses (Bedford et al. 2000) and are not easily palpable (Smith 1992). The cauda epididymis lies in a shallow cremaster sac that protrudes beyond the posterior border of the testis (Bedford et al. 2000). Males have a paired prostate, seminal vesicles, bulbourethral glands, and Cowper's-like glands (Hoefler 1994; Ivey et al. 2004). Males produce spermatozoa with modest barbs (Bedford et al. 2004).

Females have a slitlike vulva near the anal opening. The reproductive tract is in the caudal portion of the abdominal cavity. Short uterine horns open into a long vagina through the cervix (Ivey et al. 2004). Females have 2–5 pairs of mammae (Hoefler 1994); 2 pairs are on the chest with the remainder on the abdomen (Meritt 1981).

Atelerix albiventris has large eyes, ears, and whiskers with microvibrissae; these features correlate to the cortex, which shows prominent visual, auditory, and somatosensory areas in the brain (Niven and Laughlin 2008). *A. albiventris* has well-developed senses and, in contrast to historical references, its cortex has numerous sensory areas with sharp boundaries and well-organized internal topographies (Catania 2005). Mass of brain is 2.24 g (Symonds 1999). *A. albiventris* has a large rhinarium (Catania et al. 2000; Figs. 1 and 3) and a large accessory olfactory bulb (Meisami and Bhatnagar 1998).

Atelerix albiventris has short, blunt ridges on the vertebrae and a wide pelvis that allows it to curl into a ball (Kingdon 1997). The orbicularis panniculi, a circular muscle that extends along the sides and across the neck and rump, coincides exactly with the extent of the spines that are embedded in it, which helps with the ability to curl. When *A. albiventris* rolls up (Fig. 5), the orbicularis panniculi contracts and forms a bag that the body, head, and legs are brought into. The fronto-cuticularis pulls the front margin of the orbicularis panniculi, whereas the hindmost margin is attached by the coccygeo-cuticularis to the sides of the tail; these muscles pull down the sides over the shoulders and ears. A contraction of the orbicularis closes the bag (Dobson 1882). Spines become erect at opposing angles to form a dense barrier of protection (Catania et al. 2000). When the muscle relaxes, it is put back into place by a variety of small muscles beneath it (Dobson 1882).

The inner digit on the forefoot is absent or reduced into a tiny tubercle. Most young have 4 digits, but 16% of young in eastern Africa have 1 or 2 halluces on hind feet (Allen 1922).

Function.—*Atelerix albiventris*, like other species in its genus, has a low metabolic rate that can be attributed to diet, rather than being a feature evolved for energy conservation (McNab 1986). Resting metabolic rate is $0.33\ \text{ml O}_2\ \text{h}^{-1}\ \text{g}^{-1}$ (Symonds 1999). Rectal temperature is 35.1°C . Heart rate is typically 189–320 beats/min; however, the heart slows to 3–15 beats/min during hibernation (Wallach and Boever 1983).



Fig. 5.—A male *Aterix albiventris* from Mount Kasigau, Coast Province, Kenya, with the orbicularis panniculi partially contracted, demonstrating the formation of a muscular pouch into which the body, head, and legs can be enclosed. Used with permission of the photographer Troy L. Best.

The brain contains 3 somatosensory areas, 2 visual areas, and a caudolateral auditory region (of possibly 2 fields). The primary somatosensory area is located medially, whereas the 2nd somatosensory and the parietal ventral areas are located laterally. Primary and secondary visual areas are in the caudomedial cortex, while the auditory cortex forms a broad oval in the lateral and caudal cortex (Catania 2000). *A. albiventris* has macrovibrissae minimally represented in the somatosensory cortex (Brecht et al. 1997) and microvibrissae in a large area in the cortex. Microvibrissae are slightly below the rhinarium and are believed to be used in choosing food. The dense coat of spines is a sensory-motor specialization. Spines do not require fine-motor control or high-resolution sensory processing; they have a small area in the somatosensory cortex. *A. albiventris* has well-developed eyes and a large representative area in the cortex (Catania 2000).

The gastrointestinal system of *A. albiventris* consists of a simple stomach and a smooth, noncomplex colon; there is a poorly defined ileocolonic junction with no caecum (Johnson-Delaney 2006). The gastrointestinal tract is about 6.5 times the length of body (Kingdon 1974). *A. albiventris* is able to digest fiber, which indicates that cellulose probably is

eaten in the wild (Graffam et al. 1998), although invertebrates and small vertebrates comprise the majority of foods consumed (Cansdale 1960). *A. albiventris* sleeps curled up in ball or laying flat (Kingdon 1997), and it prefers 36.8°C over other temperatures (Herter 1965).

ONTOGENY AND REPRODUCTION

Ontogeny.—Parturition usually occurs during late night or early morning; dystocia and premature birth are rare (premature young lack a suckling reflex and have poorly developed immune systems—Hoefer 1994). Failure of lactation is probably an underrecognized cause of unexplained deaths of neonates (Hoefer 1994). Although relative intake of colostrum in the newborn has not been determined, immunity in newborns may be gained through the colostrum (Hoefer 1994); individuals that do not receive colostrum appear to be more susceptible to infection and disease (Smith 1995). Bacterial infections can be acquired via the placenta, umbilicus, gastrointestinal tract, or from trauma (Smith 1995). There are no immunizations recommended for this species (Smith 1995).

Young are born during any month of the year and nest in a well-lined cavity (Brodie et al. 1982; Haltenorth and Diller 1988). Neonates huddle together, especially during periods of inactivity (Smith 1995). Newborns are born blind, nearly naked, and their spines are pliable for the 1st few days after birth (Mayberly 1967). Average weight at birth is 10 g with a range of 8–13 g and a length of 20–26 mm. At birth, eyes are barely visible bumps under sealed lids, ears are erect, and pinnae are sealed. Legs are thin and fragile, and feet are formed with nails intact (Meritt 1981). Neonatal mortality is high due to desertion and cannibalism by the mother (Smith 1992).

Neonates of both sexes appear similar at birth, but the preputial opening of males migrates to near the middle of the abdomen within 24 h after birth. The vulva is only a few millimeters from the anus. In males, testicles remain intra-abdominal throughout life (Smith 1995). At birth, young are capable of vocalizing and crawling (Meritt 1981). During the 1st day, abdominal spines emerge and begin to stiffen, and after 2 days, a darker set of spines emerges (Brodie et al. 1982); spines emerge due to the changing turgidity of the initially edematous skin (Smith 1995). Young grow slowly initially, gaining only 1–2 g/day during the first 10 days of life. After this initial growth, mass increases 4–5 g/day for the next few weeks and concludes with gains of 7–9 g/day until maturity (Brodie et al. 1982).

Most mothers lick, nuzzle, and properly nurse offspring (Smith 1995). When hungry, the young actively and vigorously push at the mother to search for a nipple and feed in the prone position, most likely to avoid injuring the mother while feeding. One captive individual at the Lincoln Park Zoo in Illinois nursed from the pectoral nipples before

his eyes were open, but after they opened, he used both pectoral and abdominal teats (Meritt 1981). At 14 days of age, eyelids split but are not open; at 15 days, eyes open and there is increased activity and mobility. Deciduous teeth erupt at about 3 weeks, permanent teeth erupt at 7–9 weeks (Smith 1995), and 1st consumption of solid food occurs about 24 days after birth (Meritt 1981). Young exhibit hissing, self-anointing, and antipredator behaviors before the eyes are opened at 18–24 days (Brodie 1977). Young typically are weaned by 4–6 weeks of age (Smith 1992) and typically leave the mother in 30–45 days (Haltenorth and Diller 1988).

Atelerix albiventris reaches sexual maturity in the wild at about 1 year of age (Haltenorth and Diller 1988), but sexual maturity may be attained at 2–4 months (Smith 1992; Symonds 1999). There is no record of a reproductively active, captive-born female > 2 years of age. Only 1 wild-caught female that was in the laboratory for 33 months was able to reproduce longer (Brodie et al. 1982); wild-caught females probably are reproductively active for even shorter amounts of time.

Incest among *A. albiventris* is common in captivity. Two females were fertilized by their own offspring before being separated from them (Gregory 1975). Closely inbred animals show a higher inclination toward cannibalism, and females who display this behavior will likely do the same with future litters (Smith 1995). A 6-month-old male, a product of inbreeding, was infected with congenital erythropoietic porphyria (Wolff et al. 2005).

Most information on reproductive biology of *A. albiventris* is from captive individuals, but there are some data from wild individuals in Zambia and Rhodesia (Kingdon 1974). Young are born in November, about 2 months after adults emerge from aestivation (Kingdon 1974). Gestation lasts 30–40 days and 2–10 young may be born (average is 5—Kingdon 1974). Young are born in a nest (sometimes abandoned rodent nests are used) and are blind and almost naked with a few soft spines (Kingdon 1974). Within 2–3 days, the spines begin to grow and development of the muscular mantle is apparent (Kingdon 1974). Neonates are not capable of rolling up into a ball until 2 weeks of age because the orbicularis panniculi is not fully developed (Kingdon 1974). White infant spines are shed after a month and eyes open at 8–18 days (Kingdon 1974). The blunt fetal shape of the infant changes rapidly, and they resemble small-scale adults at 1 month (Kingdon 1974). At 40 days, they will accompany the mother on foraging trips and will eat increasing amounts of solid foods until they are completely weaned (Kingdon 1974).

Reproduction.—Data from captive animals are readily available because *Atelerix albiventris* breeds well in captivity (Brodie et al. 1982). *A. albiventris* is sexually active throughout the year with no apparent mating season (Gregory 1975). Average number of litters per year is 1, and annual fecundity is 4.5 (Symonds 1999). Females, in the

wild and captivity, are sexually active all year (Gregory 1976; Herter 1965). Body mass is not an indicator of sexual maturity (Bedford et al. 2004).

Ovulation is induced by exposure to a male (Gregory 1975; Lermayer 1992). Random injections of gonadotrophins caused a consistent occurrence of ovulation at fixed times. Ovulation occurs 16–23 h after mating. At the time of injection of gonadotrophin, about 7 or 8 eggs are ovulated (Bedford et al. 2004). Males had spermatozoa in the epididymis throughout the year (Gregory 1976). Length of time between birth of a litter and conception of the next depends upon availability of a fertile female. Length of time between initial introduction of a male and birth is 34–44 days (Meritt 1981). Detection of pregnancy is difficult, but a breeding female can be assumed to be pregnant if she gains ≥ 50 g in 1–2 weeks. During pregnancy and lactation, nutritional demands on the female are ≤ 3 times as great as during nonreproductive periods, and caloric needs can increase 5–6 times (Lermayer 1992). Wild erinaceids typically live 2–3 years and captive animals can live ≤ 10 years (Raymond and Garner 2001).

ECOLOGY

Space use.—*Atelerix albiventris* occupies a variety of terrestrial habitats including grassland, scrub (Fig. 6), savannah, suburban gardens, woodlands (Fig. 7), bush, thickets (Fig. 8), agricultural land (plantations, fields, and gardens), plains, hills, and mountains $\leq 2,000$ m in elevation (Haltenorth and Diller 1988). *A. albiventris* frequently occurs in suburban areas where it may occupy stables, food stores, and other buildings (Haltenorth and Diller 1988). These animals live in areas with dry soils (Haltenorth and Diller 1988) and are absent from deserts, marshes, and dense forests. *A. albiventris* generally requires dry shelters in matted grass, leaf litter, a rocky crevice, or a hole in the ground (Nowak 1999). This species seems to prefer grassy areas with light undergrowth (Booth 1960) and woodlands < 1,640 m in elevation (Ansell and Dowsett 1988). New shelters are chosen daily for daytime rest; however, habitual shelters are used occasionally (Kingdon 1997). Shelters are used daily unless the animal is in aestivation or rearing young (Nowak 1999).

Atelerix albiventris occurs most commonly on sandy, well-drained soils in areas where it can sleep in termitaries, rock crevices, buildings, or under tangles of brushwood or dry leaf litter. These animals show a predilection for relatively open, dry, or seasonal habitats with sparse or patchy grass cover, especially overgrazed regions with dense populations of ungulates (Kingdon 1997). These requirements are well met in suburban gardens and in many heavily grazed rangelands where there is an abundance of trampled herbage and dung to support termites and other insects. Leaf-litter thickets and coastal palm groves also are



Fig. 6.—Scrub habitat of *Atelerix albiventris* near Mount Kasigau, Coast Province, Kenya. Used with permission of the photographer Troy L. Best.



Fig. 8.—Thicket habitat of *Atelerix albiventris* at base of Mount Kasigau, Coast Province, Kenya. Used with permission of the photographer Troy L. Best.

good habitats. In eastern Africa, the species virtually disappears during the height of the dry season. In Nairobi, Kenya, *A. albiventris* is conspicuous in April–June and then again in October–November when these animals are killed on roads (Kingdon 1974). They are locally common but absent from large areas. Home range is small, usually within a 200- to 300-m radius from the burrow (Haltenorth and Diller 1988).

Diet.—Although *Atelerix albiventris* may consume plant matter (Graffam et al. 1998), it primarily preys upon invertebrates, notably termites, beetles, earthworms, millipedes, ants, grasshoppers, and slugs. They also consume



Fig. 7.—Woodland habitat of *Atelerix albiventris* at base of Mount Kasigau, Coast Province, Kenya. Used with permission of the photographer Troy L. Best.

small vertebrates including snakes, lizards, frogs, and young and eggs of ground-nesting birds (Cansdale 1960; Haltenorth and Diller 1988). Fungi, fallen fruits, snails, crabs, roots, and groundnuts also are consumed. Prey is located by sight, scent, and sound and can be located ≤ 4 cm deep in soft, loose soil (Haltenorth and Diller 1988). While hunting, *A. albiventris* moves its spines forward over the nose, leaving little exposed area (Kingdon 1974). Immobile foods often are toyed with before they are consumed, and active prey is snapped into the mouth and chewed noisily (Kingdon 1974). The muzzle is licked after eating (Haltenorth and Diller 1988).

Lizards, mice, and snakes are seized and shaken to death before being eaten. Snakes are approached with caution and are bitten severely and repeatedly by *A. albiventris* while it protects its face with spines to avoid being struck; it will continue the attack until it has broken the spinal column or disemboweled the snake (Kingdon 1974). *A. albiventris* will readily consume carrion and will scavenge roadkills at night (Okaeme and Osakwe 1988).

Diseases and parasites.—The literature is rich in accounts of disease in captive *Atelerix albiventris*, which has a variety of bacterial, fungal, and viral infections both as a host and a carrier. The most common disease in captive erinaceids is salmonellosis, with 28% of captive animals acting as asymptomatic carriers (Riley and Chomel 2005). *A. albiventris* plays a major role in transmitting salmonella tilene, a rarely encountered serotype of humans. Nevertheless, inflammatory *Tinea corporis* (ringworm) is the most commonly reported disease in this species (Rosen 2000). *A. albiventris* has exhibited a wide variety of medical conditions including thyroid C-cell carcinoma (Miller et al. 2002) and tumors (Mikaelian et al. 2004; Raymond and Garner 2001).

Animals > 3 years of age are particularly susceptible to tumors (Smith 1992).

Atelerix albiventris is highly susceptible to dermatitis from urine or fecal contamination (Smith 1992), which can be common in captive conditions, particularly if the animal is not properly cared for. Confirmed zoonoses carried by *A. albiventris* include bacterial (*Salmonella* [salmonellosis], *Yersinia* [pseudotuberculosis], *Mycobacterium marinum* [tuberculosis of the hand and wrist]), viral (rabies, herpesvirus including human *Herpes simplex*, and chandipura virus), and mycotic (*Trichophyton mentargrophytes* var. *erinacei* [arthroderma benhamiae], *Microsporum* [ectothrix ringworm fungi], dermatophytosis [ringworm], tinea barbae [fungal infection of the beard], vesiculobullous, tinea manuum [fungal infection of skin on hands], and kerion-type tinea capitis [fungal infection of the scalp]). Unilateral proptosis and orbital cellulitis also have been observed in captivity (Wheler et al. 2001).

Potential zoonoses carried by *A. albiventris* include bacterial (*Chlamydia psittaci* [psittacosis], *Coxiella burnetii* [causative agent of Q-fever], and *Yersinia pestis* [plague]), arboviruses (tickborne encephalitis, Crimean-Congo hemorrhagic fever, Tahyna virus, Bhanja virus, and paramyxovirus) protozoal (*Cryptosporidium* [coccidian protozoan parasite], and *Toxoplasma gondii* [toxoplasmosis]), and mycotic (*Candida albicans* [monilia]—Riley and Chomel 2005; Rosen 2000; Wilkes and House 1986). Animals can infect humans through direct physical contact and contact with soil in which *A. albiventris* burrows (Rosen 2000).

Atelerix albiventris is susceptible to a large number of internal and external parasites including fleas, ixodid ticks, mites (particularly *Chorioptes*), nematodes, cestodes, protozoans, including the causative agents of salmonellosis, tularemia, leptospirosis, Q-fever, foot-and-mouth disease, and cytomegalic disease (Smith 1992). They tend to have an abundance of fleas because it is extremely difficult for them to groom (Happold 1987). Helminths in the gastrointestinal tract include *Ascarops strongylina*, *Gongylonema pulchrum*, *Macracanthorhynchus hirudinaceus*, *Mesocestoides*, *Nochtiia atelerixi*, *Physocephalus sexalatus*, *Physaloptera dispar*, and *Setaria*. The insectivorous diet is the likely source of its helminths (Okaeme and Osakwe 1988).

Ectoparasites include *Amblyomma variegatum*, *Ctenocephalides crataepus* (Publicidae), *Haemaphysalis leachi leachi* (all ixodid ticks), *Rhipicephalus sanguineus*, and *Sarcoptes scabiei* (Sarcoptiformes). *A. albiventris* also harbors ticks that occur on domestic livestock: *A. strongylina*, *Gongylonema pulchrum*, and *Physocephalus sexalatus*. Most ticks are on ear lobes where spines are absent. *A. albiventris* has the potential to be a vector or host for mange (*S. scabiei*) in wild mammals, domestic animals, and humans (Okaeme and Osakwe 1985). Wild *A. albiventris* also can carry yellow fever (Happold 1987).

Interspecific interactions.—In eastern Africa, remains of *Atelerix albiventris* commonly occur in the pellets of the

Verreaux's eagle-owl (*Bubo lacteus*); its talons are capable of killing the animal in spite of its spines (Gregory 1976; Kingdon 1974). Pieces of skin from *A. albiventris* have been found impaled on branches; perhaps carried there by a scavenging shrike. A variety of other carnivores prey on *A. albiventris*, including other species of owls, ratels (*Mellivora capensis*), jackals, hyenas, and domestic dogs (Haltenorth and Diller 1988; Kingdon 1974).

Atelerix albiventris uses venom from toads (*Bufo*) to enhance its own mechanical antipredator interactions (Brodie 1977). Secretions from toads are taken into the mouth and then spread over the spines via self-anointing behavior. Presence of venom on spines would likely increase pain or potential infection of a potential predator. When *A. albiventris* attacks a toad, it bites and chews the parotid glands (containing the greatest concentration of toxins) and then distributes the poison over the spines with its own saliva (Brodie 1977).

HUSBANDRY

The friendly and inquisitive nature of *Atelerix albiventris* lends itself well to living in captivity, and it is widely used as an exhibition and demonstration animal in zoological education programs (Meritt 1981). *A. albiventris* is kept and bred by researchers, the pet trade, and private individuals. Housing should have smooth floors and walls so it can be cleaned thoroughly but is not climbed easily; wire cages are not recommended because *A. albiventris* can be injured easily. A small box or shelter should be provided inside the housing as a hiding area. Absorbent bedding, such as wood shavings or newspapers, should be provided to prevent contamination from feces and urine. A reversed day–night schedule should be kept so that caretakers can observe behavior. Temperature should be 25–30°C to prevent infection (Smith 1992).

Commercial dog or cat food, mealworms, and crickets with small amounts of fruits and vegetables will successfully maintain *A. albiventris* (Smith 1992). Insects must be included in the diet because depriving insectivores of insects may cause malnutrition and allow opportunistic pathogens to become active (Campbell 1997). Even when on a proper diet, weight should be checked often because *A. albiventris* is susceptible to both obesity and malnutrition (Smith 1992). It is important to observe drinking behavior because some individuals never learn how to drink from a water bottle (Smith 1992).

Males should be housed separately to avoid conflict (Herter 1965); females can be housed alone or with others depending on preference (Smith 1992). One male with several females is the most effective social grouping for breeding. The male must be taken away from the female before she gives birth because males are known to

cannibalize young. Females should be left alone for several weeks after birth to prevent desertion or infanticide (Smith 1992).

In the wild, *A. albiventris* is difficult to catch because of its reluctance to enter traps (Easton 1979). *A. albiventris* often is captured by hand while it crosses roads at night (Gregory 1975). In some areas of eastern Africa, this species is widely eaten as bush meat (Okaeme and Osakwe 1988). In Nigeria, holes and crevices where they live are identified, and individuals are captured by digging, pouring water into the hole, or filling the hole with smoke; when the animal comes out, it is killed for food (Okaeme et al. 1988). In eastern Africa, many superstitions surround this animal; its skin or spines often are used as fertility charms (Kingdon 1974). In Uganda and Kenya, a bumper harvest is believed to be obtained by placing the skin of erinaceids on seeds before sowing and, for maximum yields of cotton, its skin should be burned on the cotton field (Watson 1951).

BEHAVIOR

Grouping behavior.—*Aterix albiventris* is solitary except during courtship or when a female has young (Kingdon 1997). When approached by a conspecific in the wild, growling, snorting, and butting of heads occurs (Nowak 1999). Intrusion of a strange animal into the territory results in hissing and spitting (Haltcnorth and Diller 1988). Around predators, spines are erected, and an individual curls into a ball to protect its head and ventral surface (Happold 1987). When *A. albiventris* is forced to live with others in captivity, a pecking order is created (Herter 1965); however, captive males cannot be put together because they will fight and can cause serious damage to each other with their teeth and spines (Herter 1965). In captivity, *A. albiventris* will attack predators by erecting spines over the head and lunging toward the oncoming threat (Brodie 1977).

Reproductive behavior.—Courtship of *Aterix albiventris* is ritualistic (Kingdon 1974). When a female is in search of a mate, she calls with a whine (Watson 1951). Males court females by persistently following them. A male walks around a female in estrus with his snout pointed toward her, puffing, sometimes for several days; the female vigorously butts the male as she snorts and rejects him (Kingdon 1974). The male mounts the female from behind after she has flattened her spines and pressed her hindquarters out (Haltcnorth and Diller 1988; Kingdon 1974).

When placed together in captivity, courtship begins immediately and includes various noises, such as snuffles and squeals, and nipping of the spines and feet (Gregory 1975). In captivity, pregnant females should be housed separately because others in the enclosure may cannibalize neonates (Smith 1992).

After parturition, the female licks the young, eats the afterbirth, and places young on her stomach to suckle

(Kingdon 1974). Young vigorously search for a nipple; after nursing begins, swallowing noises and motion of the throat while nursing are apparent. Before eyes open, young suckle solely from pectoral nipples; after eyes open, they suckle from both abdominal and pectoral nipples (Meritt 1981). In captivity, the female is protective of her young and may lunge, hiss, or bite a human who disturbs her. She will reject, kill, and sometimes eat the young if they have been handled by humans or if she is greatly disturbed. Mothers should be left alone with young for 1–2 weeks after birth (Brodie et al. 1982).

Aterix albiventris can be both crepuscular and nocturnal and will aestivate, living on stored fat in severe hot weather (Haltcnorth and Diller 1988; Okaeme et al. 1988). In captivity, *A. albiventris* will move around during white light to urinate, defecate, feed, or change position or location, but it is most active under red light (Meritt 1981). In South Africa, aestivation usually occurs during June–September (Kingdon 1974); it is unlikely that *A. albiventris* aestivates in Nigeria (Happold 1987). Cold and lack of food can cause aestivation (Herter 1965). *A. albiventris* can aestivate for ≤ 6 weeks and will emerge if weather is warm (Nowak 1999).

Communication.—*Aterix albiventris* creates a twitter vocalization with a closed mouth that can be heard at a distance of 20 cm but hardly heard at 2 m (Gregory 1975). The twitter is heard from both sexes; however, those < 3 months old and some adults never make it. A twitter might be heard when *A. albiventris* is picked up or moved, but it also can be heard at other times. Hisses and snorts sometimes are heard when *A. albiventris* is intruded upon by domestic dogs or humans; no hiss or snort was > 1.5 kHz, but the stronger the stimulus, the louder the hiss or snort (Gregory 1975). *A. albiventris* will scream when attacked or held by its feet. Males serenade females during courtship with a birdlike call; this sound is not produced by females or by males in the absence of females. Females respond to serenading males with hisses, snorts, or evasive movements (Gregory 1975).

Miscellaneous behavior.—Self-anointing behavior occurs when *A. albiventris* comes into contact with an irritating substance. *A. albiventris* will take the substance into its mouth to create a saliva mixture that it rubs onto the spines. The reason for self-anointing is unknown (Brodie 1977) but it may be used to attract mates, or may be used by juveniles to get attention of their mother (Brockie 1976). Self-anointing is fully innate because it is performed before young open their eyes (Brodie 1977). *A. albiventris* is unable to clean well between spines (Happold 1987). In captivity, *A. albiventris* urinates and defecates in the same corner of the enclosure, not near water or nest box (Meritt 1981), and will scratch with its feet (Haltcnorth and Diller 1988). Defecation usually occurs in early evening (Meritt 1981).

Temperature is not an important factor controlling seasonal activity of *A. albiventris*; the most likely trigger

for reduced activity is an internal biochemical change associated with decline in availability and quality of food. This animal aestivates and requires thick fat reserves on which it can live while it is inactive (Kingdon 1974). Survival value of spines is enhanced by rolling into a ball when contacted or approached by a potential predator. This behavior includes erecting the spines over the head and lunging into the approaching predator (Brodie 1977).

Atelerix albiventris is terrestrial but also can climb and swim (Hoefer 1994). It typically is slow but is capable of bursts of speed (Nowak 1999). When disturbed, adults are capable of rolling into a ball; young cannot curl into a ball and their spines are soft and flexible (Haltenorth and Diller 1988; Happold 1987).

GENETICS

Atelerix albiventris has a diploid number (2n) of 48 chromosomes. Analysis of Giemsa-stained metaphase cells revealed 18 pairs of metacentric to submetacentric chromosomes. No strict acrocentric to telocentric chromosome was identified, suggesting number of autosomal arms is 92 and a fundamental number (FN) of 96. The 3rd largest chromosome is a sex chromosome (Hübner et al. 1991).

Atelerix is genetically unique from *Erinaceus* in several ways, including absence of positive heterochromatic material, a grouping of 3 small autosomal pairs (all other taxa exhibit only 2 pairs), and absence of a medium-sized acrocentric element that is present in *Erinaceus* (Hübner et al. 1991). Similarity of genetic material between *Atelerix* and *Aethechinus* (Hübner et al. 1991) support the proposal by Corbet (1988) to merge the 2 taxa into a single genus. Although that was rejected by Robbins and Setzer (1985), it has since gained acceptance (Frost et al. 1991; Hutterer 2005; Meester et al. 1986).

CONSERVATION

Atelerix albiventris is classified as “Lower Risk–Least Concern” based on a population assessment conducted in 1996 (Hutterer 2008). The species is common in suitable habitat but rarely seen (Happold 1987). *A. albiventris* is not uniformly distributed throughout its range in eastern Africa (Easton 1979).

ACKNOWLEDGMENTS

We thank W. Holland for help with the literature, D. Hurlbert and J. Whatton for providing photographs of skulls, H. Kafka for measuring the skull, C. H. Kilgore for Fig. 1, L. A. Jantz for preparing Fig. 2, and especially B. Agwanda and H. H. Thomas for the opportunity to conduct research in Kenya.

LITERATURE CITED

- ALLEN, J. A. 1922. The American Museum Congo Expedition collection of Insectivora. *Bulletin of the American Museum of Natural History* 47:1–38.
- ANDERSON, J. 1895. On a new species of the genus *Erinaceus* from Somaliland. *Proceedings of the Zoological Society of London* 1895:414–420.
- ANDERSON, J., AND W. E. DE WINTON. 1902. *Zoology of Egypt: Mammalia*. Hugh Rees, Limited, London, United Kingdom.
- ANSELL, W. F. H., AND R. J. DOWSETT. 1988. *Mammals of Malawi: an annotated check list and atlas*. Trendine Press, Saint Ives, Cornwall, United Kingdom.
- BEDFORD, J. M., O. B. MOCK, AND S. M. GOODMAN. 2004. Novelty of conception in insectivorous mammals (Liptophyla), particularly shrews. *Biological Reviews* 79:891–909.
- BEDFORD, J. M., C. B. MOCK, S. K. NAGDAS, V. P. WINFREY, AND G. E. OLSON. 2000. Reproductive characteristics of the African pygmy hedgehog, *Atelerix albiventris*. *Journal of Reproduction and Fertility* 120:143–150.
- BOOTH, A. H. 1960. *Small mammals of West Africa*. Longmans International Education, London, United Kingdom.
- BRECHT, M., B. PREILOWSKI, AND M. M. MERZENICH. 1997. Functional architecture of the mystacial vibrissae. *Behavioral Brain Research* 84:81–97.
- BROCKIE, R. 1976. Self-anointing by wild hedgehogs, *Erinaceus europaeus*, in New Zealand. *Animal Behaviour* 24:68–71.
- BRODIE, E. D., JR. 1977. Hedgehogs use toad venom in their own defense. *Nature* 268:627–628.
- BRODIE, E. D., III, E. D. BRODIE, JR., AND J. A. JOHNSON. 1982. Breeding the African hedgehog *Atelerix pruneri* in captivity. *International Zoo Yearbook* 22:195–197.
- BUTLER, P. M. 1969. Insectivores and bats from the Miocene East Africa: new material. Pp. 1–37 in *Fossil vertebrates of Africa* (L. S. B. Leakey, ed.). Academic Press, New York.
- CAMPBELL, T. 1997. Intestinal candidiasis in an African hedgehog (*Atelerix albiventris*). *Exotic Pet Practice* 2(10):79.
- CANSDALE, G. S. 1960. *Animals of West Africa*. Longmans, Green & Company, London, United Kingdom.
- CATANIA, K. C. 2000. Cortical organization in Insectivora: the parallel evolution of the sensory periphery and the brain. *Brain Behavior and Evolution* 55:311–321.
- CATANIA, K. C. 2005. Evolution of sensory specializations in insectivores. *Anatomical Record* 287(A):1038–1050.
- CATANIA, K. C., C. E. COLLINS, AND J. KAAS. 2000. Organization of sensory cortex in the East African hedgehog (*Atelerix albiventris*). *Journal of Comparative Neurology* 421:256–274.
- CORBET, G. B. 1988. The family Erinaceidae: a synthesis of its taxonomy, phylogeny, ecology and zoogeography. *Mammal Review* 18:117–172.
- DE ROCHEBRUNE, A. T. 1883. Diagnoses de quelques mammifères nouveaux ou peu connus propres à la Sénégambie. *Bulletin de la Société Philomatique de Paris, Série 7*, 7:5–11.
- DOBSON, G. E. 1882. A monograph of the Insectivora. Systematic and anatomical. J. Van Voorst, London, United Kingdom.
- EASTON, E. R. 1979. Observations on the distribution of the hedgehog (*Erinaceus albiventris*) in Tanzania. *African Journal of Ecology* 17:175–176.
- FAIRLY, J. A., J. SUCHNIAK, AND A. S. PALLER. 1999. Hedgehog hives. *Archives of Dermatology* 135:561–563.
- FITZINGER, L. J. 1866. Systematische Übersicht der Säugethiere Nordost-Afrika's mit Einschluss der arabischen Küste, des rothen Meeres, der Somäli- und der Nilquellen-Länder, südwärts bis zum vierten Grade nördlicher Breite. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse* 54(section 1):537–611.
- FITZINGER, L. J. 1867. Die natürliche Familie der Igel (Erinacei) nach dem gegenwärtigen Stande der Wissenschaft. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse* 56(section 1):844–890.
- FROST, D. R., W. C. WOZENCRAFT, AND R. S. HOFFMANN. 1991. Phylogenetic relationships of hedgehogs and gymnures (Mamma-

- lia: Insectivora: Erinaceidae). *Smithsonian Contributions to Zoology* 518:1–69.
- GOULD, G. C. 1995. Hedgehog phylogeny (Mammalia: Erinaceidae): the reciprocal illumination of the quick and the dead. *American Museum Novitates* 3131:1–45.
- GRAFFAM, W. S., M. P. FITZPATRICK, AND E. S. DIERENFELD. 1998. Fiber digestion in the African white-bellied hedgehog (*Atelerix albiventris*): a preliminary evaluation. *Journal of Nutrition* 128: 2671S–2673S.
- GREGORY, M. 1975. Observations on vocalization in the central African hedgehog, *Erinaceus albiventris*, including a courtship call. *Mammalia* 39:1–7.
- GREGORY, M. 1976. Notes on the central African hedgehog *Erinaceus albiventris* in the Nairobi area. *East African Wildlife Journal* 14: 177–179.
- HALTENORTH, T., AND H. DILLER. 1988. *The Collins field guide to the mammals of Africa including Madagascar*. Stephen Green Press, Lexington, Massachusetts.
- HAPPOLD, D. C. D. 1987. *The mammals of Nigeria*. Clarendon Press, Oxford, United Kingdom.
- HELLER, E. 1910. New species of insectivores from British East Africa, Uganda, and the Sudan. *Smithsonian Miscellaneous Collections* 56(15):1–8.
- HERTER, K. 1965. *Hedgehogs, a comprehensive study*. Phoenix House, London, United Kingdom.
- HOEFER, H. L. 1994. Hedgehogs. *Veterinary Clinic of North America Small Animal Practice* 24:113–120.
- HÜBNER, R., T. MADDALENA, AND W. PODUSCHKA. 1991. The karyotype of the middle-African hedgehog *Atelerix albiventris* Wagner, 1841 and its cytotaxonomical relationships to other Erinaceinae (Insectivora: Erinaceidae). *Genetica* 83:243–246.
- HUTTERER, R. 2005. Order Erinaceomorpha. Pp. 212–219 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- HUTTERER, R. 2008. *Atelerix albiventris*. International Union for Conservation of Nature and Natural Resources Red list of threatened species. Version 2009.2. www.iucnredlist.org, accessed 20 November 2009.
- IVEY, C. T., D. E. CARR, AND M. D. EUBANKS. 2004. Effects of inbreeding in *Mimulus guttatus* on tolerance to herbivory in natural environments. *Ecology* 85:567–574.
- JOHNSON-DELANEY, C. A. 2006. Anatomy and physiology of the gastrointestinal system of the ferret and selected exotic carnivores. *Proceedings from the Association of Avian Veterinarians* 2006: 29–38.
- KINGDON, J. 1974. *East African mammals: an atlas of evolution in Africa*. Vol. 2A. Academic Press, London, United Kingdom.
- KINGDON, J. 1997. *The Kingdon field guide to African mammals*. Academic Press, San Diego, California.
- LEREBoullet, D. A. 1842. Coup d'œil general sur les mammifères de l'Algérie qui font partie du musée de Strasbourg. Chapitre premier. Pp. 3–8 in *Notes et renseignements sur les animaux vertébrés de l'Algérie qui font partie du musée de Strasbourg*. Première partie—mammifères (G. L. Duvernoy and D. A. Lereboullet, eds.). *Mémoires de la Société du Muséum d'Histoire Naturelle de Strasbourg* 3(2):1–73.
- LERMAYER, R. M. 1992. African pygmy hedgehogs: latest pet sensation. *Live Animal Trade and Transport Magazine* December, 45–48.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Holmiae, Impensis Direct. Laurentii Salvii, Stockholm, Sweden.
- MAYBERLY, A. 1967. *The game animals of southern Africa*. Thomas Nelson & Sons, Johannesburg, South Africa.
- MCNAB, B. K. 1986. The influence of food habits on the energetics of eutherian mammals. *Ecological Monographs* 56:1–19.
- MEESTER, J., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. *Transvaal Museum Monograph* 5:1–359.
- MEISAMI, E., AND K. P. BHATNAGAR. 1998. Structure and diversity in mammalian accessory olfactory bulb. *Microscopy Research and Technique* 43:476–499.
- MERRITT, D. A., JR. 1981. Husbandry, reproduction and behaviour of the West African hedgehog at Lincoln Park Zoo. *International Zoo Yearbook* 21:128–131.
- MIKAELIAN, I., D. R. REAVILL, AND A. PRACTICE. 2004. Spontaneous proliferative lesions and tumors of the uterus of captive African hedgehogs (*Atelerix albiventris*). *Journal of Zoo and Wildlife Medicine* 35:216–220.
- MILLER, D. L., E. L. STYER, J. K. STOBÆUS, AND T. M. NORTON. 2002. Thyroid C-cell carcinoma in an African pygmy hedgehog (*Atelerix albiventris*). *Journal of Zoo and Wildlife Medicine* 33:392–396.
- MORALES, A., AND J. ROFES. 2008. Early evidence for the Algerian hedgehog in Europe. *Journal of Zoology (London)* 274:9–12.
- NIVEN, J. E., AND S. B. LAUGHLIN. 2008. Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology* 211:1792–1804.
- NOWAK, R. M. 1999. *Walker's mammals of the world*. 6th ed. Johns Hopkins University Press, Baltimore, Maryland.
- OKAEME, A. N., AND M. E. OSAKWE. 1985. Ectoparasites of the African hedgehog *Atelerix albiventris* (Wagner) in the Kainji Lake area of Nigeria. *African Journal of Ecology* 23:167–169.
- OKAEME, A. N., AND M. E. OSAKWE. 1988. Gastro-intestinal helminthes and food of the African hedgehog *Atelerix albiventris* (Wagner) in the Kainji Lake area of Nigeria. *African Journal of Ecology* 26: 239–241.
- OKAEME, A. N., O. A. OKEYOYIN, AND J. O. AYANDA. 1988. Habitat utilisation of the African hedgehog in the Kainji Lake area. *Nigerian Field Naturalist* 53:179–182.
- POMEL, A. 1848. Etudes sur les carnassiers insectivores (extrait). Seconde partie. Classification des insectivores. *Archives des Sciences Physiques et Naturelles Genève* 9:244–251.
- RAYMOND, J. T., AND M. M. GARNER. 2001. Spontaneous tumors in captive African hedgehogs (*Atelerix albiventris*): a retrospective study. *Journal of Comparative Pathology* 124:128–133.
- REEVE, N. 1994. *Hedgehogs*. T. & A. D. Poyser, Limited, London, United Kingdom.
- RHOADS, S. N. 1896. Mammals collected by Dr. A. Donaldson Smith during his expedition to Lake Rudolf, Africa. *Proceedings of the Academy of Natural Sciences of Philadelphia* 48:517–546.
- RILEY, P. Y., AND B. B. CHOMEL. 2005. Hedgehog zoonoses. *Emerging Infectious Diseases* 11:1–5.
- ROBBINS, C. B., AND H. W. SETZER. 1985. Morphometrics and distinctness of the hedgehog genera (Insectivora: Erinaceidae). *Proceedings of the Biological Society of Washington* 98:112–120.
- ROMER, A. S. 1945. *Vertebrate paleontology*. 2nd ed. University of Chicago Press, Chicago, Illinois.
- ROSEN, T. 2000. Hazardous hedgehogs. *Southern Medical Journal* 93: 936–938.
- SETZER, H. W. 1953. A new hedgehog from Africa. *Journal of the Washington Academy of Sciences* 43:237–238.
- SETZER, H. W. 1956. Mammals of the Anglo-Egyptian Sudan. *Proceedings of the United States National Museum* 106(3377): 447–587.
- SMITH, A. 1831. An epitome of African zoology; or, a concise description of the objects of the animal kingdom inhabiting Africa, its islands and seas. *South African Quarterly Journal* 2:49–64.
- SMITH, A. J. 1992. Husbandry and medicine of African hedgehogs (*Atelerix albiventris*). *Journal of Small Exotic Animal Medicine* 2:21–28.
- SMITH, A. J. 1995. Neonatology of the hedgehog (*Atelerix albiventris*). *Journal of Small Exotic Animal Medicine* 3:15–18.
- SUNDEVALL, C. J. 1842. Öfersigt af släget *Erinaceus*. *Kungliga Svenska Vetenskaps-Akademiens Handlingar, Stockholm* 1841: 215–239 (not seen, cited in Frost et al. 1991).
- SYMONDS, M. R. E. 1999. Life histories of the Insectivora: the role of phylogeny, metabolism and sex differences. *Journal of the Zoological Society of London* 249:315–337.
- THOMAS, O. 1910. Further new African mammals. *Annals and Magazine of Natural History, Series 8*, 5:191–202.
- THOMAS, O. 1918a. The generic division of the hedgehogs. *Annals and Magazine of Natural History, Series 9*, 1:193–196.
- THOMAS, O. 1918b. Four new species of hedgehog. *Annals and Magazine of Natural History, Series 9*, 1:230–233.
- THOMAS, O., AND R. C. WROUGHTON. 1907. New mammals from Lake Chad and the Congo, mostly from the collections made during the

- Alexander–Gosling Expedition. *Annals and Magazine of Natural History*, Series 7, 19:370–387.
- WAGNER, J. A. 1841. Die Raubthiere. Pp. 14–23 in *Die Säugethiere in Abbildungen nach der Natur mit Geschreibergen* (J. C. D. von Schreber, ed.). Supplementband 2:1–558.
- WALLACH, J. D., AND W. J. BOEVER. 1983. *Diseases of exotic animals*. W. B. Saunders, Philadelphia, Pennsylvania.
- WATSON, J. M. 1951. The wild mammals of Teso and Karemojo. *Uganda Journal* 15:93–95.
- WHEELER, C. L., B. H. GRAHN, AND A. M. POCKNELL. 2001. Unilateral proptosis and orbital cellulitis in eight African hedgehogs (*Atelerix albiventris*). *Journal of Zoo and Wildlife Medicine* 32:236–241.
- WILKES, C. R., AND J. A. HOUSE. 1986. Susceptibility of various animals to the vesiculoviruses Isfahan and Chandipura. *Journal of Hygiene* 97:359–368.
- WOLFF, C., P. CORRADINI, AND G. CORTES. 2005. Congenital erythropoietic porphyria in an African hedgehog (*Atelerix albiventris*). *Journal of Zoo and Wildlife Medicine* 36:323–325.

Associate Editors of this account were DAVID M. LESLIE, JR., and PAMELA OWEN. Synonymies were reviewed by ALFRED L. GARDNER. Editor was MEREDITH J. HAMILTON.