



Litocranius walleri (Artiodactyla: Bovidae)

EVA V. BÄRMANN,[✉] ARIANA N. KLAPPERT, AND AUGUSTIN CHEN

www.mammalogy.org

Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany; e.baermann@leibniz-zfmk.de (EVB); s6arklap@uni-bonn.de (ANK)

University of Strasbourg, Rue Blaise Pascal, 67081 Strasbourg, France (AC)

Present address of AC: Ludwig-Maximilians-Universität Munich, Division of Evolutionary Biology, Faculty of Biology, Geschwister-Scholl-Platz 1, 80539 München, Germany; chen-augustin@hotmail.fr (AC)

Abstract: *Litocranius walleri* (Brooke, 1878) is a bovid commonly called the gerenuk. It is a medium-sized antelope closely related to gazelles and springbok, but unlike these it has low-crowned teeth. *L. walleri* is the only species in the genus *Litocranius*. It is commonly found in dry thornbush savannah in northeastern Africa, where it feeds almost exclusively on thorny shrubs and trees while frequently using a bipedal stance. *L. walleri* is classified as “Near Threatened” (NT) by the International Union for Conservation of Nature and Natural Resources (IUCN) because its population trends are decreasing.

Key words: gerenuk, giraffe-necked gazelle, *Litocranius sclateri*, Waller’s gazelle

Synonymies completed 1 September 2020

DOI: 10.1093/mspecies/seab007

Version of Record, first published online June 26, 2021, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for this publication: urn:lsid:zoobank.org:pub:4A183328-7E9D-49B0-9146-BEFCDB26019F

Litocranius Kohl, 1886

Gazella Brooke, 1878:929. Part.

Litocranius Kohl, 1886:79. Type species *Gazella walleri* Brooke, 1878, by original designation.

Lithocranius Thomas, 1891. Unjustified emendation (see “Nomenclatural Notes”).

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, family Bovidae, subfamily Antilopinae, tribe Antilopini. *Litocranius* is monotypic (Grubb 2005:682).

Litocranius walleri (Brooke, 1878)

Gerenuk

Gazella walleri Brooke, 1878:929, pl. LVI. Type locality “mainland of Africa, north of the island of Zanzibar, about lat. 3° S. and long. 38° E”; restricted to the vicinity of Chisimaio by Grubb (2002; see “Nomenclatural Notes”).

Litocranius (*Gazella*) *walleri*: Kohl, 1886:79. First use of current name combination.



Fig. 1.—Adult male *Litocranius walleri* in Buffalo Springs National Reserve, Kenya. Photograph by Dr. Frank Zachos used with permission.

Lithocranius sclateri Neumann, 1899:21. Type locality “das nördliche Somali-Land [= northern Somalia]” (see “Nomenclatural Notes”).

Lithocranius walleri sclateri: Rothschild 1902:473. Name combination.

CONTEXT AND CONTENT. Context as for genus. *Litocranius walleri* has two subspecies (Grubb 2002).

L. w. sclateri Neumann, 1899. See above.

L. w. walleri (Brooke, 1878). See above.

NOMENCLATURE NOTES. In the original description of the genus, Kohl (1886) did not comment on the etymology of the name. However, he emphasized the extraordinary elongated and flattened appearance of the skull compared with gazelles that justified generic distinction. Later authors assumed that the name was based on the “solid stony character of the cranium (λίθος = lapis [gemstone])” (Sclater and Thomas 1898:227). Therefore, they concluded that there was a misprint in the original description and changed the name to *Lithocranius*. In 1933, Krumbiegel clarified the situation by demonstrating that the species was named according to its long and flattened skull (λίτός = plain, modest, simple, frugal—Krumbiegel 1933). The name appears twice in the original description, so a misprint seems unlikely.

In the original species description, Brooke (1878:929) gave the type locality as “mainland of Africa, north of the island of Zanzibar, about lat. 3° S. and long. 38° E,” therefore in Kenya. Sclater and Thomas (1898) refer to their correspondence with Sir John Kirk, who had employed the hunters who collected the type specimens (one of the three skulls is preserved in the Natural History Museum in London, BM [British Museum of Natural History] 1897.7.29.1—Lydekker 1914). Kirk stated that they were collected “on the coast near the River Juba in Southern Somaliland” (Sclater and Thomas 1898:230) and that he later shot other specimens at the same location. One of these specimens collected by Kirk is also preserved in the Natural History Museum, with the locality Kismayu (now Kismayo), a town located near the mouth of the Jubba River. Grubb (2002:539) therefore restricted the type locality of *Litocranius walleri* to “the vicinity of Chisimaio” in southern Somalia. Nevertheless, not all authors followed the argument of Sclater and Thomas and still cite the original type locality in Kenya (e.g., Neumann 1899; Schomber 1963).

Sclater (1884) states that the type specimens of *L. w. sclateri* (two skins) came from “Somali -land, vicinity of Berberah.” The name *gerenuk* derives from the Somali word “*garanuug*.”

DIAGNOSIS

Litocranius walleri (Fig. 1) differs from the closely related gazelles and springbok by its very elongated legs, neck, ears, and skull (especially in the part behind the horns—Brooke 1878; Kohl 1886; Sclater and Thomas 1898). The skull (Fig. 2) has a flattened skull-roof, hardly curving down toward the back as in gazelles. The extremely elongated supraoccipital bone reaches the length of the parietals. It forms a cone-shaped hump that

extends beyond the sloping part of the occiput (Kohl 1886). The braincase of males is heavily ossified and carries extremely heavy horns (Kingdon 1982). *L. walleri* is the only bovid with low-crowned teeth (hypsodonty index = 1.32—Janis 1986). Contrary to all other gazelles (exception: mountain gazelle [*Gazella gazella*]), the premaxillae of *L. walleri* do not reach the nasals (Kohl 1886). The closely related dibatag (*Ammodorcas clarkei*) can be regarded as showing an intermediated morphology between gazelles and *L. walleri*, in terms of skull elongation and tooth reduction (Thomas 1891; Lydekker 1914). The dibatag can, however, be easily distinguished from *L. walleri* by its very different horn shape (horns curve backward and then upward and forward, similar to the horns of reedbuck [*Redunca*]). *L. walleri* is unique in its feeding behavior, as it frequently adapts a bipedal stance for reaching browse at up to 2 m off the ground (Menges 1887; Sclater and Thomas 1898).

GENERAL CHARACTERS

Litocranius walleri has characteristic facial markings (Fig. 1): a broad white ring around the eyes; black preorbital glands anterior to the eyes; white lips, chin, and throat; and long ears with black-and-white markings on the inside. A dark-brown stripe extends from between the ears and over the neck; the stripe broadens to a saddle along the entire rump, before narrowing again toward the tail. The flanks and outer parts of the legs are light brown, and the belly and inner parts of the legs are white. A thin light stripe can often be found between the saddle and the flanks. *L. walleri* has a narrow, white rump patch and dark brown to black knee-tufts. The tail is white near the base and has a black tip, and the underside is black and hairless (Sclater 1884; Schomber 1963; Estes 1992). Grubb (2002:541) notes that seven skins from Tanzania, Kenya, and southern Somalia have a “band of reversed hairs directed towards the head on the dorsal midline of the neck,” and that he never observed this character in specimens from northern Somalia, which could indicate a potential differentiation of the two subspecies.

There is a marked sexual dimorphism in *L. walleri*. Males are larger and more massive, especially in the anterior body region. The neck of males has the same width throughout the entire length, whereas the neck of females is generally more slender and decreases in width toward the head (Ullrich 1963). Males have heavy lyre-shaped horns (32–44 cm) with strong annulations that start to grow relatively late during ontogeny (after about 5 months); females are hornless (Sclater and Thomas 1898).

External measurements (cm) of *L. walleri* were: total length (snout to tail), 165–195; head–body length, males 155–160 and females 140–155; tail length, 22–35; height at withers, males 89–105 and females 80–100. Weight varies from 31.2 to 52 kg in males and 28.5 to 45 kg in females (Schomber 1963; Kingdon 1982). The northern subspecies, *L. w. sclateri*, is noticeably larger than the nominate subspecies (Sclater and Thomas 1898; Neumann 1899; Schomber 1963). *L. w. walleri* has shorter

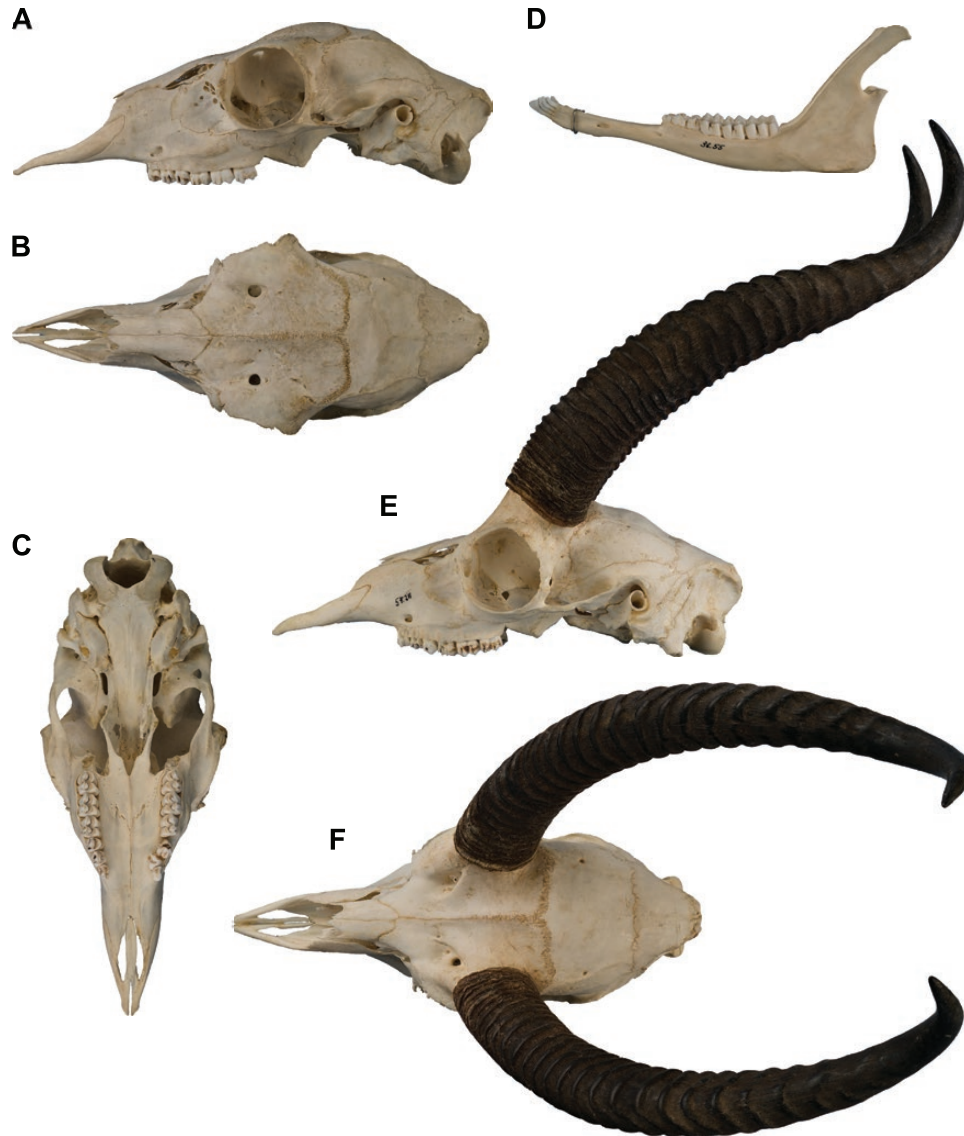


Fig. 2.—Skulls of adult *Litocranius walleri* housed in the mammal collection at Zoological Research Museum Alexander Koenig in Bonn. (A–D) Female (ZFMK_MAM_1936.0055 from northern Tanzania, west of Kilimanjaro, condyle-basal length [CBL] = 209 mm); (E, F) male (ZFMK_MAM_1957.0211 from Kenya, Garba Tula, north of the Tana river, CBL = 208 mm). (A, E) Lateral view; (B, F) dorsal view; (C) ventral view; (D) mandible.

nasals and premaxillae, a more reddish coat color, and black knee-tufts, as opposed to brown knee-tufts in *L. w. sclateri*. A geographic cline from north to south may exist in these traits (Neumann 1899; Schomber 1963).

Measurements for 44 skulls from various museum collections (London, Florence, New York, Nairobi) were provided by Schomber (1963). Grubb (2002) reused these data together with measurements from additional specimens from the Natural History Museum, London and provided the mean \pm SD (mm) for the two subspecies according to his definition of their geographic boundaries (see “Distribution”). Measurements for *L. w. walleri* (24 males and seven females) and *L. w. sclateri* (10 males and five females), respectively, were: greatest length of skull males, 231.58 ± 6.68 and 251.25 ± 4.35 ; greatest length

of skull females, 210.86 ± 5.27 and 227.30 ± 3.38 ; nasal length males, 58.57 ± 6.40 and 69.45 ± 3.21 ; nasal length females, 53.29 ± 4.57 and 61.54 ± 6.71 ; premaxillary length males, 58.06 ± 3.11 and 65.58 ± 2.91 ; premaxillary length females, 53.00 ± 3.00 and 59.92 ± 2.99 . Neumann (1899) also postulated a difference in toothrow lengths between the two subspecies, but Schomber (1963) did not confirm this. Mean tooth measurements are thus presented for all specimens combined (mm; range in parentheses): length of upper molar row, 30.8 (28–34.3); length of upper premolar row, 21.2 (19–23); length of lower molar row, 33.2 (31–37.7); length of lower premolar row, 19.3 (17–22.3).

Limb bone lengths (mm) were provided by McMahon (1975; mean \pm SD) and Christiansen (1999; mean values in parentheses): humerus, (165.0); ulna, 175 ± 19 ; radius, (221.0);

femur, 213 ± 20.5 (207.0); tibia, 282 ± 18.7 (266.0); and metatarsus, 279 ± 14.8 . [McMahon \(1975\)](#) also provided a measurement for the length of the humerus (276 ± 16.2 mm); however, this was probably a mistake (could be 176?) because the humerus is markedly shorter than the radius in *Litocranius*.

DISTRIBUTION

Litocranius walleri is native to the Somali-Masai arid zone from southern Djibouti, eastern Ethiopia, Somalia, and Kenya to northwestern Tanzania ([Leuthold 1971](#); [IUCN SSC](#)

[Antelope Specialist Group 2016](#)) at elevations below 1,200 m ([Fig. 3](#)). It presumably still occurs throughout its historical distribution, although recent information is not available from all countries inhabited by *L. walleri*. It is debated whether a gap in the species' distribution exists. [Schomber \(1963\)](#) stated that a gap exists in the distribution of the species between the Tana and Sabaki rivers in eastern Kenya, and that this gap separates the two subspecies of *L. walleri*, *L. w. sclateri* north of the Tana, and the smaller *L. w. walleri* south of the Sabaki River. [Leuthold \(1971\)](#) clarified that the area of the potential species distribution gap is simply understudied due to its difficult accessibility. He cited personal communications



Fig. 3.—Geographic range of *Litocranius walleri* (based on [IUCN 2016](#)). Map is based on a customizable map of the Horn of Africa available on [d-maps.com](https://d-maps.com/carte.php?num_car=25596&lang=de) (https://d-maps.com/carte.php?num_car=25596&lang=de). The Sabaki River was added using the map “Tsavo national park map en.png” by Lencer, available on commons.wikimedia.org. Coordinates were added using the map of Kenya available on www.ducksters.com.

with game wardens that confirm the presence of *L. walleri* throughout the area. Leuthold also studied *L. walleri* in Tsavo East National Park that lies north of the Sabaki River. Grubb (2002) postulated that *L. w. sclateri* only occurs in northern Somalia and Ethiopia, separated from *L. w. walleri* by the mountain range extending from the Churcher Highlands of Ethiopia to the Goolis Mountains of northern Somalia.

A petrograph exists at Hôsh (Wâdi Sab'er Rigâl) near Silwah on the eastern bank of the Nile River in Upper Egypt. It shows a man holding a *L. walleri* on a leash and was dated to 4,000–2,900 BCE (6,000–4,900 years ago—Winkler 1939). This coincides with an African Humid Period (11,700–4,400 years ago) when subtropical North Africa was much greener than today (Claussen et al. 2017). *L. walleri*, in association with other elements of the tropical fauna from Sudan, was able to extend its distribution into the Sahara, until the subsequent aridification led to a shrinking of its distribution to its present size (Schomber 1963). No fossils of *L. walleri* are known.

FORM AND FUNCTION

Form.—*Litocranius walleri* has the typical glands of gazelline antelopes: preorbital glands (very prominent in males, excreting a thick oily secretion), carpal glands with knee-tufts, and interdigital glands (Estes 1992; Sokolov et al. 1994). Primary and secondary hair follicles are present in the integument at a ratio of 1:1 and are interspersed. The secondary hairs are very short, and their bulbs do not extend below the level of the bilobular sebaceous glands associated with the primary hair follicles. The sweat glands of *L. walleri* have convoluted shapes and are similar in size to those of oryx (*Oryx beisa*) and lesser kudu (*Ammelaphus*—Jenkinson and Nay 1975). A detailed histological description of the integument of *L. walleri* in different body areas is provided by Sokolov et al. (1994).

Females have four mammae (Estes 1992). The content of the milk of one captive female was reported by Grzimek (1959) as: 2.1% fat, 4.0% lactose, 0.78% albumin fraction, 5.63–7.7% casein, but these values should be taken with caution because the female died next day from a deficiency of vitamin C and K.

The dental formula of *L. walleri* is i 0/3, c 0/1, p 3/3, m 3/3, total 32. Although *L. walleri* is classified as a browser (hypso-donty index = 1.32, mesowear score = 0.87—Kaiser et al. 2013), its occlusal morphology is more similar to frugivores due to the thickened enamel (measured on the M2—Heywood 2010). *L. walleri* has relatively small frontal sinuses that terminate anterior to the supraorbital canal. The sinuses are restricted to the lateral position of the frontal bone and are separated from the lacrimal sinuses by a thin bony lamina (Farke 2010).

The erect stance in *L. walleri* is possible due to a pronounced lumbar lordosis permitted by a reduction in the spinous process of the lumbar vertebrae (Richter 1970; Cartmill and Brown 2017). Apart from this, other morphological features usually attributed to bipedalism (e.g., expanded cranial sector of the acetabular

semilunar surface) are not present in *L. walleri* (Cartmill and Brown 2017).

Richter (1970) compared the proportions of the limb bones in various gazelline antelopes and concluded that the elongation of the limbs in *Litocranius* primarily stems from an elongation of the metapodials; however, the humerus and radius are also relatively longer than in other antelope species. He also noted that *Litocranius* has the longest forelegs of all gazelline antelopes (90.5% the length of the hind legs) and is the only genus where the metacarpals are longer than the metatarsals. Compared with other antelopes, the limb bones of *Litocranius* are extremely thin-walled. Currey and Alexander (1985) calculated the ratio *K* between the outer and the inner diameter of the bone for various mammalian species (*K* = 0 when bone is solid, *K* approaches 1 when bone is very thin-walled). The values for *L. walleri* were: femur 0.73; tibia 0.54; metatarsus 0.58; humerus 0.67; and metacarpus 0.63. The values for the femur, metacarpus, and metatarsus of *L. walleri* are the highest among mammals in general, even including small mammals that tend to have thinner bone walls.

The vertebral formula of *L. walleri* is 7 C, 13 T, 6 L, 4 S, 7 Ca, total 37 (number of caudal vertebrae according to a drawing in Kingdon 1982:428). The seventh cervical vertebra has a robust, comb-like processus spinosus that is rather thin and spiky in other antelopes (Richter 1970). The surfaces of the vertebral joints in the neck are very large and arranged almost horizontally, allowing for extensive movement in the sagittal plane.

Despite its facultative bipedalism, the musculature of the hind leg of *Litocranius* only shows minor differences compared with Thomson's gazelle (*Eudorcas thomsonii*) or domestic bovids (Richter 1970). Values for the distribution and diameter of red, intermediate, and white muscle fibers in the longissimus dorsi muscle of *L. walleri* and other antelopes are provided by Stickland (1979). In comparison to other bovids, *L. walleri* has the highest percent distribution of red muscle fibers (50.5% versus 11.1–28.2% in other bovids) and the lowest distribution of white muscle fibers (27.5% versus 34.3–44.8%) and intermediate muscle fibers (22.0% versus 28.0–54.6%). The diameters of the respective fibers (red, 40.6 µm; white, 70.3 µm; intermediate, 55.3 µm) lie within the range of those in other bovid species.

Tongue measurements for *L. walleri* were provided by Meier et al. (2016). Mean values (cm) for three individuals were: tongue length, 13.2; torus length, 5.5; torus width, 2.5; corpus length, 7.7; maximum width of corpus, 2.2; minimum width of corpus, 2.0; free portion, 3.9 (29%). *L. walleri* therefore has the smallest relative tongue length (in terms of total length, torus length, and corpus length in relation to body mass) of all analyzed species that have 0% grass in their diet (Meier et al. 2016).

The aorta of *L. walleri* shows paired ostia shaped like narrow slits for all intercostal arteries. The renal arteries have a common origin in the aorta (Sikes 1967). The ostial collars have a characteristic cup-like shape, that can also be found in other artiodactyls with a sloping back, adapting a more vertical stance when feeding, for example, klipspringer

(*Oreotragus*), giraffe (*Giraffa*), and steenbok (*Raphicerus campestris*)—Sikes 1969).

Brain weights of two adult *L. walleri* were reported to be 105 and 130 g; body weights of the respective animals were 38 and 42 kg (Oboussier and Schliemann 1966). Friant (1938) described the fetal brain of *L. walleri* and made the following observations: posterior groove of rhinal sulcus more pronounced than the anterior; ectosylvia anterior more visible than the posterior; lateral sulcus and suprasylvia clearly visible; coronal sulcus noticeable, and presylvia slightly visible. For the splenial sulcus, only the median part was visible. Friant (1938) suggested that, similar to *Gazella*, the crucial sulcus would be the only part of the splenial that extends to the external part of the hemispheres in the adult brain of *Litocranius*.

Average weights of salivary glands of *L. walleri* are 59.2 g for the parotid gland ($n = 4$) and 27.8 g for the mandibular gland ($n = 2$)—Hofmann et al. 2008). Maloij et al. (1982) described the digestive system of 10 wild *L. walleri* (mean % \pm SE): weight of the gastrointestinal contents relative to the body mass, $12.1 \pm 0.8\%$; weight of each gut region (as % of total gut weight) was reticulorumen, $78.1 \pm 0.9\%$; small intestine, $5.6 \pm 0.8\%$; and cecum plus colon, $16.3 \pm 0.7\%$. The analyzed *L. walleri* had a mean blood glucose concentration of 67.3 ± 1.8 mg/100 ml and a serum urea nitrogen concentration of 48.0 ± 1.6 mg/100 ml. The rumen of *L. walleri* is relatively evenly papillated (Hofmann and Stewart 1972), with surface enlargement factors of 7.5 in the dorsal rumen, 12.0 in the ventral rumen, and 19.0 in the atrium. These values are typical for browsing ruminants (Clauss et al. 2009).

Litocranius walleri has a bicornuate uterus, and the placenta occupies both uterine horns. It has a polycotyledonary placenta (typical for most ungulates), with an epitheliochorial relation to the maternal tissues. Benirschke (2008) examined two placentas: one belonged to an immature fetus and had > 80 cotyledons and an umbilical cord of 5 cm length, and the other belonged to a full-term fetus and had 48 cotyledons arranged in four rows and an umbilical cord of 15 cm length.

Function.—Clemens and Maloij (1983, 1984) studied the concentration, absorption, and secretion of fluids, electrolytes, and organic acids in the digestive system of African wild ruminants. They found that the percentage of dry matter in the distal colon (where fecal pellets are formed) of *L. walleri* was 65%, indicating a water resorption within the colon of 65.1%. This was the highest value of all analyzed species in these studies (average percentage of dry matter in the colon in other bovid species ranged from 15.0 to 42.2). The resorption and secretion of electrolytes was found to be quite variable among the species, and the sample size for most species was low (e.g., $n = 3$ for *L. walleri*), so results have to be viewed with caution. *L. walleri* absorbed 38 mg/100 ml of sodium, 4.5 mg/100 ml of potassium, 11.1 mg/100 ml of chloride, and 19.1 mmol/l of volatile fatty acids (Clemens and Maloij 1983).

In an adrenocorticotrophic hormone (ATCH) challenge test, the concentration of fecal glucocorticoid metabolites (stress-hormone derivatives) of *L. walleri* was measured using the ICN 07-120102 corticosterone antibody. An excretion peak of about 230 ng/g occurred about 12 h after the ATCH injection, and a second prolonged peak of 115–95 ng/g about 38–60 h after the injection (Wasser et al. 2000).

ONTOGENY AND REPRODUCTION

Litocranius walleri shows nonseasonal reproduction (Piening Schuler et al. 2009a), with births occurring year-round. Only singletons are born, but one female can have two births in 1 year (Schomber 1963), with an average calving interval of 248 days (222–321) in captivity (Houston et al. 1988). Body weights of neonatal *L. walleri* are 2.8–3.4 kg (Piening Schuler et al. 2009b). Weights recorded 24 h after birth were 2.3–3.8 kg (mean 3.1 kg—Houston et al. 1988). Two hand-reared *L. walleri* accepted milk until 5 and 9 months old (Schomber 1963). Weaning of two other hand-reared young at the St. Louis Zoo occurred at 49 and 89 days (Houston et al. 1988). Minimum age of conception (recorded in a zoo) was 11 months, but females usually reach sexual maturity at 1.5–2 years (Kirchshofer 1963; Houston et al. 1988). Male offspring start to produce semen at 12 months of age and are pubertal at 18 months (Penfold et al. 2005); they part with their mothers at 1–1.5 years and become territorial at 2.75–3.5 years (Leuthold 1978b).

In a study on artificial insemination, Penfold et al. (2005) studied the reproductive physiology of *L. walleri*. The testosterone level of captive adult males did not show seasonal variation. Mean testes volume was 22.2 ± 1.7 cm³. Semen was collected from anesthetized males using electroejaculation, and no seasonal variation was found in total sperm number ($463.0 \pm 88.0 \times 10^6$), sperm motility ($60 \pm 4.4\%$), and normal sperm morphology ($40.0 \pm 4.7\%$). Interestingly, this high number of malformed spermatozoa (60%) was also found in wild *L. walleri* (Penfold et al. 2005). Mean length of the ovarian cycle is 18.7 ± 0.9 days (Penfold et al. 2005). Pregnancy lasts for about 210 days (range: 194–221 days—Houston et al. 1988). One female treated with artificial insemination using cryopreserved spermatozoa delivered a stillborn young after 213 days (Penfold et al. 2005). There is one reported case of an ectopic pregnancy carried to full-term in a captive *L. walleri* with fetal viability confirmed through day 213. Fetal membranes were attached to the omentum (Helmick and Citino 2001).

ECOLOGY

Population characteristics.—Density of *Litocranius walleri* was 0.5–1/km² in Tsavo National Park (Leuthold 1978a) and 0.01 in Kenya (Okello et al. 2016); the latter value was recorded after severe droughts in the studied area. Piening Schuler et al. (2009b) reported survival rates of semicaptive

parent-reared *L. walleri*: 74% survived the first week of life, 65% the first month, and 49% the first year. Survival of hand-reared *L. walleri* was slightly higher (87% for the first week, 87% for the first month, and 53% for the first year). Survival of female offspring (eight of nine) was much higher than survival of male offspring (one of seven) in captive *L. walleri* at Frankfurt Zoo (Kirchshofer 1963). Sex ratio of subadults and adults in Tsavo National Park was 65 males:100 females (Leuthold 1978a). The maximum age of a *L. walleri* in captivity was 17 years and 4 months (Weigl 2005).

Space use.—*Litocranius walleri* uses a variety of habitats with woody vegetation, being most common in dry, flat thornbush, and it avoids dense bush, thickets, tall woodland, and open savanna. Density increases with aridity and distance from permanent water in Tsavo National Park, possibly due to reduced resource competition with more water-dependent browsers (Estes 1992).

Permanent territories of adult males are 0.8–2.8 km² (average 2.1; Tsavo National Park—Leuthold 1971) but can be as large as 4 km² (Leuthold 1978b). Usually these territories do not overlap and often have no common boundaries. Home ranges of females are of similar size (1.4–3.4 km²) and could partially or completely overlap with one male territory (Leuthold 1978a, 1978b). *L. walleri* is sedentary, but home-range shifts of a few kilometers can occur. Vacant territories might not be reoccupied for several months (Leuthold 1971).

Diet.—*Litocranius walleri* is a browser and not known to eat grass or even small herbs (Leuthold 1970). It is adapted to feed selectively on small-leaved, thorny shrubs and trees (e.g., *Acacia*, *Commiphora*), possessing a long pointed tongue, mobile lips, spoon-shaped lower incisor row, and eyes protected by long lashes and vibrissae. Up to 68 different species of plants in the diet of *L. walleri* were reported in Tsavo National Park, including some fruit (Leuthold 1970). The diet varies throughout the year, with many climbing plants (e.g., *Dalechampia ipomoeifolia*, *Thunbergia guerkeana*) and deciduous trees (e.g., *Premna resinosa*, *Hymenodictyon parvifolium*) in the rainy season, and predominantly evergreen plants such as *Thylachium thomasii*, *Maerua endlichii*, and *Boscia coriacea* in the dry season. Succulents are not found in the diet of *L. walleri* (Leuthold 1971).

Litocranius walleri is usually not observed drinking in captivity, and only a few cases were reported (Iles 1955 [not seen, cited in Schomber 1963]; Rühmekorf (by letter) in Schomber 1963). Only one documented case of two wild *L. walleri* drinking from a puddle exists (Hagen 1975), and most authors assume that *L. walleri* does not drink (Leuthold 1971; Kingdon 1982). In captivity, it has been observed repeatedly that females drink urine of males in the days following parturition (Backhaus 1960), a behavior assumed to supplement the increased demand for water after giving birth. This behavior followed a certain ritual (“Harnzeremoniell”) that incorporated aspects of mating behavior (e.g., “Laufschlag” and mating march). Nevertheless, Leuthold (1971) reported that he never observed such behavior in wild *L. walleri*.

Diseases and parasites.—Contagious caprine pleuropneumonia, caused by *Mycoplasma capricolum capripneumoniae*, was found in one captive adult *Litocranius walleri* (Arif et al. 2007). Another captive male was diagnosed to have died from eastern equine encephalomyelitis, the first reported case of this virus in an exotic ruminant species (Young et al. 1994). *L. walleri* is susceptible to malignant catarrhal fever, a clinicopathological syndrome caused by the alcelaphine herpesvirus 1 (Metzler 1991).

Diarrhea was a frequent medical problem in semicaptive *L. walleri*. In Al Wabra Wildlife Preservation, it occurred in 34 of 85 individuals within 7 years, causing deaths of two adults and eight juveniles. Infectious agents were *Escherichia coli* (11 cases), *Coccidia* sp. (five cases), and *Giardia* (one case—Hammer et al. 2008). In a study on bovine tuberculosis, two out of five *L. walleri* tested were positive for bacteria from the *Mycobacterium terrae* complex and one for *Nocardia testacea* (Tschopp et al. 2010).

The coccidium *Eimeria walleri* was described as a new species from a captive *L. walleri* in London (Prasad 1960). Black et al. (1999) found the blood serum of *L. walleri* to be fully supportive of the replication of the African trypanosome *Trypanosoma brucei* clone 1 and clone 22.

A captive-born 2-year-old male died from congestive heart failure caused by congenital hematocysts (Citino and Herron 1990). Lloyd and Stidworthy (2011) reported on severe cases of osteofluorosis in several captive *L. walleri*, caused by high levels of fluoride in a commercial feed. Lice in the genera *Bumalinia* (*Tricholipeurus*) and *Linognathus* were found on one wild *L. walleri* (Hopkins 1949).

Interspecific interactions.—*Litocranius walleri* coexists with a range of Somali arid-zone ungulate species, including giraffe (*Giraffa camelopardalis*), lesser kudu (*Ammelaphus* sp.), Grant’s gazelle (*Gazella granti*), beisa oryx (*Oryx beisa*), and Grevy’s zebra (*Equus grevyi*—Said 2003). Hirola (*Beatragus hunteri*—Ruso 2017) and Burchell’s zebra (*Equus quagga burchellii*—Regassa 2013) can also be found in association with *L. walleri*.

Presence of livestock can significantly reduce numbers of *L. walleri* (Said 2003), and changes in vegetation due to increased numbers of elephants (*Loxodonta africana*) can result in a decline of *L. walleri* (Parker 1983 [not seen, cited in Arsenault and Owen-Smith 2002]).

Cheetahs (*Acinonyx jubatus*—Graham 1966), hyenas (*Crocuta crocuta* and *Hyaena hyaena*—Fourvel et al. 2015), lions (*Panthera leo*—Patterson et al. 2004), and leopards (*Panthera pardus*) prey on *L. walleri*, but leopards seem to prefer other prey (Hayward et al. 2006). Wild dogs (*Lycaon pictus*) also occasionally kill *L. walleri* (Woodroffe et al. 2007).

HUSBANDRY

Litocranius walleri has occurred in zoos at least since the 1930s. The St. Louis Zoo, a facility known for its well-established

management of *L. walleri*, first displayed a female in 1937 (Houston et al. 1988). Breeding groups, however, were only established in the 1970s when 30 *L. walleri* were imported from Kenya to the United States (St. Louis Zoo, Los Angeles Zoo, Bush Gardens, and Gladys Porter Zoo—Barnes 2002). Of those imported, 28 founded the Association of Zoos and Aquariums (AZA) population, from which all existing individuals are descended (with the exception of individuals that might result from artificial insemination with Kenyan imported sperm—Penfold et al. 2005). Thus, the entire Association of Zoos and Aquariums population belongs to the subspecies *L. w. walleri*.

The current European zoo population derives from the United States population, and just a few individuals can today be seen in the Berlin Tierpark Friedrichsfelde and the Berlin Zoo. Historically, both subspecies were on display in Europe, with breeding populations of *L. w. sclateri* at Frankfurt Zoo from 1956 to 1979 (Scherpner 2011) and Antwerpen Zoo from 1957 to 1965 (Zootierliste 2019).

Litocranius walleri is often kept in small groups of 4–7 individuals (Penfold et al. 2005); breeding groups can consist of one male and two females. Young males are removed from the herd at an age of 9–14 months due to intraspecific aggression from the breeding male. Young males can be housed in bachelor herds and mixed with other species (Houston et al. 1988). Species that have been mixed with *L. walleri* include ungulates, such as the eastern bongo (*Tragelaphus eurycerus isaaci*), Guenther's dik-dik (*Madoqua guentheri*), Soemmerring's gazelle (*Nanger soemmerringii*), and giraffe, and birds, such as the common ostrich (*Struthio camelus*) and southern ground hornbill (*Bucorvus leadbeateri*—Association of Zoos and Aquariums Ungulate TAGs 2017).

Challenges for the maintenance of *L. walleri* in captivity include its fragile and often nervous nature (Thomas et al. 1986), high death rates, and decreasing gene diversity (Penfold et al. 2005; Association of Zoos and Aquariums Antelope and Giraffe Taxon Advisory 2014). Injuries due to flight behavior can be decreased via large enclosures, fencing with yielding material, and habituation of keepers (Hammer et al. 2008). *L. walleri* receives vitamin E, penicillin, and monoclonal antibodies against *Escherichia coli* to reduce various illnesses often found in captive individuals (Thomas et al. 1986). For invasive procedures, *L. walleri* can be anesthetized using a combination of medetomidine (40–60 µg/kg) and ketamine (3 mg/kg) administered with a blow gun (Penfold et al. 2005; Pas 2014), and anesthesia can be reversed using atipamezole (0.25 ± 0.1 mg/kg—Penfold et al. 2005).

Housing for *L. walleri* should have indoor stalls and an outdoor yard. Indoor stalls need to be maintained at 20°C throughout the winter. *L. walleri* needs to be kept inside when outside temperatures drop below 18°C (Houston et al. 1988) and when it is raining. The outdoor yard must have a separation from the visitors, such as a railing with 1.4 m distance to the yard (Houston et al. 1988) or via moat coupled with a fence or a wall of 80 cm in height (Scherpner 1971). The St. Louis Zoo provided

L. walleri with alfalfa hay, fresh browse when in season (e.g., maple [*Acer*], mulberry [*Morus*], and sycamore [*Platanus*]), pelleted dairy chow, and string beans. Supplements such as vitamin A and Rocavit-E (Roche Chemical Division, Hoffman-La Roche Inc., Nutley, New Jersey) vitamins were added to the diet (Houston et al. 1988).

BEHAVIOR

Grouping behavior.—*Litocranius walleri* can occur in herds of up to 30 individuals (Eisenberg 1966) but typically form smaller groups of 3–4 animals with no more than one adult male or just adult females and their young. Subadult males are frequently found alone or associated with other males of the same age, sometimes also with adult females (Leuthold 1978b). Adult males are usually territorial and can occupy the territory for several years (Leuthold 1978a). Adult males without a territory stay solitary or occasionally join groups of subadult males. In general, associations of individuals seem to be temporary, loose, and mainly caused by an overlap of home ranges (Leuthold 1978b).

Intimidation behavior occurs in the form of head-shaking and swift lowering of the head (Leuthold 1978b). Combat between males starts after both contestants bow their heads. They then creep up on one another and clash horns. Both try to twist their head away, followed by movement of the head left and right. The opponent will mirror the head movements until one starts to charge again (Walther 1961). During combat, both males vigorously swish their tails. Subadult and juvenile males engage in play fighting with other subadults (Leuthold 1978b) or adults (Walther 1961).

Young males and females display submissiveness by lifting the tail and curling it over the back (Leuthold 1978b). In captivity, female *L. walleri* will lay down with the front legs and neck flat on the ground as a clear sign of submission (Walther 1961).

Litocranius walleri shows a typical contact behavior of rubbing their heads against each other's jaw. This has been observed between two or more adult females and occasionally between adult males (Leuthold 1978b). Captive individuals have been observed licking and nibbling one another (Walther 1958).

Reproductive behavior.—Mating ceremonies begin with the male approaching the female with his nose held up high. Males then display a behavior called the “Laufschlag” that is typical for many antelopes. *Litocranius walleri*, however, does this in a slower and more pronounced manner. The male extends its front leg between the hind legs and front legs of the female, and the male's leg can be completely extended. He will do this until the female either accepts or declines mating. The male occasionally will use this behavior to “kick” the female up from a laying position. Females uncomfortable with the sexual advances flap their ears; progression of this behavior is shaking of the head with ears and nose raised. The female

might also run or hold her head up high with her ears laid back. A female accepting sexual advances walks ahead of the male, proceeds to urinate, and later lowers her head in preparation of copulation. The male will let the urine run over his snout and flehm. Males use their antorbital glands to mark the female (Walther 1958). During copulation, both partners stand with head and neck erect, and the forelegs of the male loosely hanging down (Ullrich 1963). Ullrich (1963) further stated that he often saw males with inflated necks during the breeding season (in June 1955 in Tanzania) and interpreted this as part of courtship display.

A detailed account of the birth of an *L. walleri* in the Frankfurt Zoo (and comparable time frames of a second birth) was given by Kirchshofer (1963): 30 min (14 min) after the rupture of fetal membranes, the head of the fawn appeared, and it was born 55 min (1.5 h) later. The mother immediately cleaned the newborn and ate the fetal membranes and umbilical cord. After 20 min, the newborn tried to stand for the first time and succeeded in doing so 1 h after birth, with first successful steps 40 min later. The placenta was delivered 2 h and 50 min (same in the second case) after the neonate and immediately eaten by the mother. Ten minutes later, the neonate drank for the first time. Neonate and mother communicate with soft calls (“knätschen”). Birth-related events at St. Louis Zoo were summarized (means and ranges) by Houston et al. (1988): total duration of labor 6.6 (1.5–16) h, neonate standing after 1.4 (0.75–3) h, and neonate suckling for the first time after 0.75–4 h.

After birth, the mother leads her young to a hiding place. This might be repeated for the next few days. After the first week, young start to choose their hiding site, thus beginning the hiding phase. Mothers end each hiding phase by walking toward the hiding site and at 15–20 m away start to call for their young. Daytime hiding sites are typically among small trees or bushes, and nighttime hiding sites consist of dry branches. In the first 4 weeks, young *L. walleri* hide for 9–9.5 h, separated from their mothers that can be up to 1.5 km away. After 2 months, the hiding phase is reduced to 5 h/day, and at 3 months, hiding is changed to resting behavior (Reif and Klingel 1991). At 5 months, the young stays with the mother. Due to the long resting hours, suckling mainly takes place in the morning (0700–0800 h) and evening (1800–1900 h—Leuthold 1978b).

Communication.—An adult male *Litocranius walleri* marks its territory by placing secretions of the antorbital gland on bare wooden twigs (Gosling 1981). The marks of one territorial male in two consecutive years were placed along a 2- to 3-km-long band bordering an oval-shaped area of 12–30 ha within his territory, with radiating lines of scent marks stretching outward. The marked area therefore is much smaller than the territory itself (Gosling 1981). The average height of marks is about 116 cm (Leuthold 1978b). Marks consist of small deposits in spherical forms of up to 1 cm diameter. Large marks likely are the result of repeated application of secretion on the same spot (Gosling 1981). Scent marks are commonly found on plant species such as *Delonix elata* and *Premna resinosa*, particularly

on sites most likely to be found by conspecifics, for example, along trails (Gosling 1981). Leuthold (1978b) mentioned that all marked shrubs had been fed upon, thus marking is frequently correlated with feeding. Marking frequency is 0.6–3.7 times/h, highest in the late afternoon, but increasing markedly after territorial fights (Leuthold 1978b). In captivity, *L. walleri* is known to mark fencing, wire, pencils, and fingers when tame (Gosling 1981). Males have been observed to perform a shrub-horning behavior in which they thrash shrubs with their horns. In captivity males are known to thrash their horns against the ground as well (Leuthold 1978b).

Similar to all species in Antilopini, adult *L. walleri* usually urinate and defecate in sequence, adopting very conspicuous body postures with legs stretched far behind during urination, and a low crouched position when defecating on the exact same spot (Estes 1992). This urination–defecation sequence is often preceded with scraping the ground with their forelegs, and can be accompanied with antorbital gland marking. Frequency of urination in males (0.6 times/h) is significantly higher than in females (0.4 times/h), and it can be assumed that urination by males plays a role in communication (Leuthold 1978b). Nevertheless, *L. walleri* does not maintain dung middens as some other antelopes do, for example, oribi (*Ourebia ourebi*), bontebok (*Damaliscus pygargus*), and impala (*Aepyceros melampus*—Estes 1992).

When alarmed, *L. walleri* makes a low short noise (Sclater and Thomas 1898). Abdominal contractions are clearly visible during this process (Leuthold 1978b). Under predation risk, it will hide or flee. Hiding consists of a typical body position where it will stretch its neck up high, with nose in the air and ears held flat on the head (Walther 1958). Flight consists of a gallop, and sometimes individuals will expose their white rump patches by spreading the hair of the perineal area (Leuthold 1978b).

Miscellaneous behavior.—*Litocranius walleri* is famous for its feeding behavior because it frequently browses bipedally (Fig. 4; Menges 1887; Sclater and Thomas 1898) and is even able to walk a few steps sideways on its hind legs while browsing (Leuthold 1971). In a hand-reared *L. walleri*, without contact to conspecifics, this behavior started to occur within the first 2 weeks after birth, with the first successful attempt at the age of 1 month (Leuthold and Leuthold 1973). *L. walleri* uses rotary galloping when running (after the second hindfoot, the forefoot on the same body side touches the ground—Biancardi and Minetti 2012).

Daytime activity of *L. walleri* is negatively correlated with ambient temperature: the higher the temperature, the less time spent feeding (Robinson and Owen-Smith 2004). *L. walleri* is known to lie down and wait during rain, probably to reduce heat loss. The basic daytime rhythm shows an alternation between feeding and ruminating bouts. Social environment, reproductive status, weather conditions, and external disturbances likely modify daytime activities (Leuthold and Leuthold 1978).



Fig. 4.—Adult female *Litocranius walleri* showing the typical behavior of feeding bipedally. Buffalo Springs National Reserve, Kenya. Photograph by Dr. Frank Zachos used with permission.

GENETICS

Litocranius walleri has a diploid number ($2n$) of 60 acrocentric chromosomes and a fundamental number (FN) of 60 (Wurster and Benirschke 1968). The autosomes are acrocentrics or subacrocentrics, the X chromosome is a large acrocentric and the Y chromosome is a medium acrocentric (Wurster and Benirschke 1968). The genome size of one *L. walleri* male was estimated to be 7.32 pg of DNA per cell nucleus, based on flow cytometric analysis (Krishan et al. 2005); this value is slightly larger than values published for other species of gazelles.

Protein (and gene) sequences known for *L. walleri* include cytochrome-*c* oxidase subunit 1, 2, 3 (*COXI*, *COXII*, *COXIII*); cytochrome *b* (*CYTB*); NADH-ubiquinone oxidoreductase chain 1, 2, 3, 4, 4L, 5, 6 (*ND1*, *ND2*, *ND3*, *ND4*, *ND4L*, *ND5*, *ND6*); integrin beta (*integrin beta1*); ATP

synthase subunit a (*ATP6*); ATP synthase protein 8 (*ATP8*); beta spectrin (*SPTBNI*); thyroptin beta chain (*THYR*); protein kinase C iota (*PRKCI*); and Kappa-casein (*KCAS*; <http://www.uniprot.org/uniprot/Q95MR4>). Two complete mitochondrial genomes were sequenced by Hassanin et al. (2012) and are available on GenBank (www.ncbi.nlm.nih.gov/genbank; accession number NC_020716.1 and JN632653.1).

CONSERVATION

Litocranius walleri is classified as “Near Threatened” (NT) by the International Union for Conservation of Nature and Natural Resources, and about 10% of all *L. walleri* occur in protected areas in Ethiopia (e.g., Mago National Park, Awash National Park), Kenya (e.g., Tsavo National Park, Sibiloi National Park, Meru National Park, Samburu Game Reserve), and Tanzania (e.g., Mkomazi Game Reserve and Tarangire National Park—IUCN SSC Antelope Specialist Group 2016). Threats include anthropogenic activities such as hunting (Funaioli and Simonetta 1966), habitat fragmentation, and deforestation (Holst et al. 2013). *L. walleri* is hunted commercially and traditionally for bushmeat and skins. Traditionally, it is hunted with bow and arrow (Grayson et al. 2007). Hunting by tourists has been increasing, and in some areas the *L. walleri* populations have been fairly heavily affected (e.g., Mkomazi in Tanzania up to 10% of the population—Caro et al. 1998). The skin of *L. walleri* is exported from Somalia (Funaioli and Simonetta 1966).

Human conflicts contribute directly to the hunting of *L. walleri* in Kenya and Somalia, as young men (referred to as warriors) in Kenya (Squires et al. 2016) and military in Somalia (Funaioli and Simonetta 1966) are known to hunt *L. walleri* for fresh meat. Actions to counter these impacts include establishment of nature reserves with strict no-hunting zones (Funaioli and Simonetta 1966) and education and social activities (Squires et al. 2016). *L. walleri* is an ideal species to combine conservation and ecotourism efforts because it is known to attract tourists and can therefore help in establishing conservation tourism by acting as a flagship species (Holst et al. 2013). Some *L. walleri* live close to densely inhabited areas, such as Djibouti city, so it can easily be used in conservation education (Holst et al. 2013). Lastly, there is a positive effect of other social activities on conservation, for example, in parts of Kenya where the introduction of soccer decreased the time warriors spent killing wildlife (Squires et al. 2016). Additional improvements to conservation efforts have occurred with the collaboration of the Kenyan and Tanzanian governments on monitoring and assessing of animals along their border (Okello et al. 2015). Conservation efforts protecting the habitat of the endangered Grevy’s zebra (*Equus grevyi*) also help protect *L. walleri* living in that area (Said 2003).

ACKNOWLEDGMENTS

We thank Dr. Frank Zachos for providing photographs of living gerenuks in Buffalo Springs National Reserve, Kenya. Two anonymous reviewers made corrections and suggestions that improved the manuscript. The authors appreciate the constructive comments of the editor, Meredith Hamilton.

LITERATURE CITED

- ARIF, A., J. SCHULZ, F. THIAUCOURT, A. TAHA, AND S. HAMMER. 2007. Contagious caprine pleuropneumonia outbreak in captive wild ungulates at Al Wabra Wildlife Preservation, State of Qatar. *Journal of Zoo and Wildlife Medicine* 38:93–96.
- ARSENAULT, R., AND N. OWEN-SMITH. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313–318.
- AZA [ASSOCIATION OF ZOOS AND AQUARIUMS] ANTELOPE AND GIRAFFE TAXON ADVISORY. 2014. AZA antelope and giraffe TAG regional collection plan. Association of Zoos and Aquariums, Silver Springs, Maryland.
- AZA [ASSOCIATION OF ZOOS AND AQUARIUMS] UNGULATE TAGS. 2017. Ungulate taxon advisory groups mixed-species exhibit manual. Association of Zoos and Aquariums, Silver Springs, Maryland.
- BACKHAUS, D. 1960. Zur Anpassung der Giraffengazelle, *Litocranius walleri* Brooke, 1878, an trockene Lebensräume. *Säugetierkundliche Mitteilungen* 9:43–45.
- BARNES, R. G. 2002. 2001 Regional studbook, North American studbook. 10th ed. Los Angeles Zoo, Los Angeles, California.
- BENIRSCHKE, K. 2008. Comparative placentation. <http://placentation.ucsd.edu/gerenuks.htm>. Accessed 20 July 2019.
- BIANCARDI, C. M., AND A. E. MINETTI. 2012. Biomechanical determinants of transverse and rotary gallop in cursorial mammals. *Journal of Experimental Biology* 215:4144–4156.
- BLACK, S. J., ET AL. 1999. Anti-*Trypanosoma brucei* activity of nonprimate zoo sera. *Journal of Parasitology* 85:48–53.
- BROOKE, V. 1878. On a new species of gazelle from Western Africa. *Proceedings of the Zoological Society of London* 1878:929–930.
- CARO, T. M., ET AL. 1998. The impact of tourist hunting on large mammals in Tanzania: an initial assessment. *African Journal of Ecology* 36:321–346.
- CARTMILL, M., AND K. BROWN. 2017. Posture, locomotion and bipedality: the case of the gerenuk (*Litocranius walleri*). Pp. 53–70 in *Human paleontology and prehistory* (A. Marom and E. Hovers, eds.). Springer, New York.
- CHRISTIANSEN, P. 1999. Scaling of mammalian long bones: small and large mammals compared. *Journal of Zoology (London)* 247:333–348.
- CITINO, S. B., AND A. J. HERRON. 1990. Clinical challenge: case 1. *Journal of Zoo and Wildlife Medicine* 21:371–372.
- CLAUSS, M., R. R. HOFMANN, J. FICKEL, W. J. STREICH, AND J. HUMMEL. 2009. The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. *Journal of Morphology* 270:929–942.
- CLAUSSEN, M., A. DALLMEYER, AND J. BADER. 2017. Theory and modeling of the African Humid Period and the Green Sahara. In *The Oxford research encyclopedia of climate science*. doi:10.1093/acref/ore/9780190228620.013.532. Accessed 19 August 2019.
- CLEMENS, E. T., AND G. M. O. MALOYI. 1983. Digestive physiology of East African wild ruminants. *Comparative Biochemistry and Physiology, A. Comparative Physiology* 76:319–333.
- CLEMENS, E. T., AND G. M. O. MALOYI. 1984. Colonic absorption and secretion of fluids, electrolytes and organic acids in East African wild ruminants. *Comparative Biochemistry and Physiology, A. Comparative Physiology* 77:51–56.
- CURREY, J. D., AND R. MCN. ALEXANDER. 1985. The thickness of the walls of tubular bones. *Journal of Zoology (London)* 206:453–468.
- EISENBERG, J. F. 1966. The social organizations of mammals. *Handbuch der Zoologie* 8:1–92.
- ESTES, R. D. 1992. *The behavior guide to African mammals*. University of California Press, Berkeley.
- FARKE, A. A. 2010. Evolution and functional morphology of the frontal sinuses in Bovidae (Mammalia: Artiodactyla), and implications for the evolution of cranial pneumaticity. *Zoological Journal of the Linnean Society* 159:988–1014.
- FOURVEL, J.-B., P. FOSSE, AND G. AVERY. 2015. Spotted, striped or brown? Taphonomic studies at dens of extant hyaenas in eastern and southern Africa. *Quaternary International* 369:38–50.
- FRIANT, M. 1938. Un stade embryonnaire du cerveau du *Litocranius* (Antilopinae). *Anatomischer Anzeiger* 86:411–414.
- FUNAIOLI, U., AND A. M. SIMONETTA. 1966. The mammalian fauna of the Somali Republic: status and conservation problems. *Monitore Zoologico Italiano. Supplemento* 1:285–347.
- GOSLING, L. M. 1981. Demarkation in a gerenuk territory: an economic approach. *Zeitschrift für Tierpsychologie* 56:305–322.
- GRAHAM, A. 1966. East African Wild Life Society cheetah survey: extracts from the report by wildlife services. *African Journal of Ecology* 4:50–55.
- GRAYSON, C. E., M. FRENCH, M. J. O'BRIEN, AND D. S. GLOVER. 2007. *Traditional archery from six continents: the Charles E. Grayson collection*. University of Missouri Press, Columbia.
- GRUBB, P. 2002. Types, type locality and subspecies of the gerenuk *Litocranius walleri* (Artiodactyla: Bovidae). *Journal of Zoology (London)* 257:530–543.
- GRUBB, P. 2005. Family Bovidae. Pp. 673–722 in *Mammal species of the world, a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed., Vol. 1. John Hopkins University Press, Baltimore, Maryland.
- GRZIMEK, B. 1959. Die Milch der Giraffengazellen, *Litocranius walleri* (Brooke). *Der Zoologische Garten, NF* 24:283–284.
- HAGEN, H. 1975. Zum Trinkverhalten der Giraffengazellen (gerenuk), (*Litocranius walleri* Brooke, 1878). *Zeitschrift für Säugetierkunde* 40:54–57.
- HAMMER, C., ET AL. 2008. Medical management and pathology of captive gerenuk (*Litocranius walleri*) at Al Wabra Wildlife Preservation (AWWP) from 2001 to 2006. Pp. 349–351 in *Proceedings of the 7th European Association of Zoo- and Wildlife Veterinarians (EAZWV) scientific meeting, 30 April–3 May 2008, Leipzig, Germany*.
- HASSANIN, A., ET AL. 2012. Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies* 335:32–50.
- HAYWARD, M. W., P. HENSCHL, J. O'BRIEN, M. HOFMEYER, G. BALME, AND G. I. H. KERLEY. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270:298–313.
- HELMICK, K. E., AND S. B. CITINO. 2001. Surgical resolution of an ectopic pregnancy in a captive gerenuk (*Litocranius walleri walleri*). *Journal of Zoo and Wildlife Medicine* 32:503–508.
- HEYWOOD, J. J. N. 2010. Functional anatomy of bovid upper molar occlusal surfaces with respect to diet. *Journal of Zoology* 281:1–11.
- HOFMANN, R. R., AND D. R. M. STEWART. 1972. Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* 36:226–240.
- HOFMANN, R. R., W. J. STREICH, J. FICKEL, J. HUMMEL, AND M. CLAUSS. 2008. Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. *Journal of Morphology* 269:240–257.
- HOLST, B., ET AL. 2013. *Conserving Djibouti's priority land animals - a seminar and conservation workshop. Final report*. IUCN SSC Conservation Specialist Breeding Group, Gland, Switzerland.
- HOPKINS, G. H. E. 1949. The host-associations of the lice of mammals. *Proceedings of the Zoological Society of London* 119:387–604.
- HOUSTON, E. W., B. W. READ, AND R. E. MILLER. 1988. Captive management of the gerenuk at the St Louis Zoo. *International Zoo Yearbook* 27:319–326.

- ILES, G. 1955. The gerenuk or giraffe-necked gazelle. International Zoo News, Wassenaar, The Netherlands (not seen cited in Schomber 1963).
- IUCN SSC ANTELOPE SPECIALIST GROUP. 2016. *Litocranius walleri*. The IUCN Red List of Threatened Species 2016: e.T12142A50190292. <https://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T12142A50190292.en>. Accessed 29 August 2019.
- JANIS, C. M. 1986. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. Pp. 367–387 in *Teeth revisited: proceedings of the VIIIth international symposium on dental morphology*, Paris 1986 (D. E. Russell, J.-P. Santoro, and D. Sigogneau-Russell, eds.). Mémoires du Muséum National d'Histoire Naturelle (Paris), serie C, 53.
- JENKINSON, D. M., AND T. NAY. 1975. The sweat glands and hair follicles of different species of Bovidae. *Australian Journal of Biological Sciences* 28:55–68.
- KAISER, T. M., D. W. H. MÜLLER, M. FORTELIUS, E. SCHULZ, D. CODRON, AND M. CLAUSS. 2013. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Review* 43:34–46.
- KINGDON, J. 1982. *East African mammals: an atlas of evolution in Africa*, vol. 3, part D. University of Chicago Press, Chicago, Illinois.
- KIRCHSHOFER, R. 1963. Das Verhalten der Giraffengazelle, Elenantilope und des Flachlandtapirs bei der Geburt; einige Bemerkungen zur Vermehrungsrate und Generationsfolge dieser Arten im Frankfurter Zoo. *Zeitschrift für Tierpsychologie* 20:143–159.
- KOHL, F. F. 1886. Ueber neue und seltene Antilopen des k. k. naturhistorischen Hofmuseums. *Annalen des K.K. Naturhistorischen Hofmuseums* 1:75–86.
- KRISHAN, A., P. DANDEKAR, N. NATHAN, R. HAMELIK, C. MILLER, AND J. SHAW. 2005. DNA index, genome size, and electronic nuclear volume of vertebrates from the Miami Metro Zoo. *Cytometry Part A* 65A:26–34.
- KRUMBIEGEL, I. 1933. Notiz zur Benennung der Giraffengazelle (*Litocranius walleri* Brooke). *Der Zoologische Garten* NF 6:116–118.
- LEUTHOLD, B. M., AND W. LEUTHOLD. 1978. Daytime activity patterns of gerenuk and giraffe in Tsavo National Park, Kenya. *African Journal of Ecology* 16:231–243.
- LEUTHOLD, W. 1970. Preliminary observations on food habits of gerenuk in Tsavo National Park, Kenya. *East African Wildlife Journal* 8:73–84.
- LEUTHOLD, W. 1971. Freilandbeobachtungen an Giraffengazellen (*Litocranius walleri*) im Tsavo-Nationalpark, Kenia. *Zeitschrift für Säugetierkunde* 36:19–37.
- LEUTHOLD, W. 1978a. On the ecology of the gerenuk *Litocranius walleri*. *Journal of Animal Ecology* 47:561–580.
- LEUTHOLD, W. 1978b. On social organization and behaviour of the gerenuk *Litocranius walleri* (Brooke 1878). *Zeitschrift für Tierpsychologie* 47:194–216.
- LEUTHOLD, W., AND B. M. LEUTHOLD 1973. Notes on the behaviour of two young antelopes reared in captivity. *Zeitschrift für Tierpsychologie* 32:418–424.
- LLOYD, C., AND M. F. STIDWORTHY. 2011. Osteofluorosis in captive gerenuk (*Litocranius walleri*) and bongo (*Tragelaphus eurycerus isaaci*) antelope. *Journal of Zoo and Wildlife Medicine* 42:113–117.
- LYDEKKER, R. 1914. *Catalogue of the ungulate mammals in the British Museum (Natural History)*. Vol. III. Printed by order of the trustees of the British Museum, London, United Kingdom.
- MALOY, G. M. O., E. T. CLEMENS, AND J. M. Z. KAMAU. 1982. Aspects of digestion and in vitro rumen fermentation rate in six species of East African wild ruminants. *Journal of Zoology (London)* 197:345–353.
- MCMAHON, T. A. 1975. Allometry and biomechanics: limb bones in adult ungulates. *The American Naturalist* 109:547–563.
- MEIER, A. R., U. SCHMUCK, C. MELORO, M. CLAUSS, AND R. R. HOFMANN. 2016. Convergence of macroscopic tongue anatomy in ruminants and scaling relationships with body mass or tongue length. *Journal of Morphology* 277:351–362.
- MENGES, J. 1887. Bemerkungen über die Gazella walleri des nördlichen Somalilandes. *Der Zoologische Garten* 2:54–59.
- METZLER, A. E. 1991. The malignant catarrhal fever complex. *Comparative Immunology, Microbiology & Infectious Diseases* 14:107–124.
- NEUMANN, O. 1899. Drei neue afrikanische Säugethiere. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1899:15–22.
- OBOUSSIER, H., AND H. SCHLIEMANN. 1966. Hirn-Körpergewichtsbeziehungen bei Boviden. *Zeitschrift für Säugetierkunde* 31:464–471.
- OKELLO, M. M., ET AL. 2015. The status of key large mammals in the Kenya – Tanzania borderland: a comparative analysis and conservation implications. *International Journal of Biodiversity and Conservation* 7:267–276.
- OKELLO, M. M., ET AL. 2016. Population density of elephants and other key large herbivores in the Amboseli ecosystem of Kenya in relation to droughts. *Journal of Arid Environments* 135:64–74.
- PARKER, I. S. C. 1983. The Tsavo story: an ecological case history. Pp. 37–50 in *Management of large mammals in African conservation areas*. Proceeding of a symposium held in Pretoria, Pretoria, South Africa, 29–30 April 1982 (R. N. Owen-Smith, ed.). HAUM Educational Publishers, Pretoria, South Africa.
- PAS, A. 2014. Gazelle and small antelope. Pp. 843–856 in *Zoo animal and wildlife immobilization and anesthesia* (G. West, D. Heard, and N. Caulkett, eds.). 2nd ed. John Wiley & Sons, Hoboken, New Jersey.
- PATTERSON, B. D., S. M. KASIKI, E. SELEMPO, AND R. W. KAYS. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119:507–516.
- PENFOLD, L. M., S. L. MONFORT, B. A. WOLFE, S. B. CITINO, AND D. E. WILDT. 2005. Reproductive physiology and artificial insemination studies in wild and captive gerenuk (*Litocranius walleri walleri*). *Reproduction, Fertility and Development* 17:707–714.
- PIENING SCHULER, Y., C. HAMMER, M. CLAUSS, AND S. HAMMER. 2009a. Birth seasonality in captive bovids at Al Wabra Wildlife Preservation (AWWP), Qatar. Pp. 297–303 in *Proceedings of the International Conference on Diseases of Zoo and Wild Animals* (G. Wibbelt, P. Kretschmar, and H. Hofer, eds.), 20–24 May 2009, Berlin, Germany. Leibniz Institute for Zoo and Wildlife.
- PIENING SCHULER, Y., C. HAMMER, AND S. HAMMER. 2009b. Body mass development and survival rate in hand- and parent-reared Bovidae at Al Wabra Wildlife Preservation (AWWP), Qatar. Pp. 291–296 in *Proceedings of the International Conference on Diseases of Zoo and Wild Animals* (G. Wibbelt, P. Kretschmar, and H. Hofer, eds.), 20–24 May 2009, Berlin, Germany.
- PRASAD, H. 1960. Studies on the *Coccidia* of some mammals of the families Bovidae, Cervidae and Camelidae. *Zeitschrift für Parasitenkunde* 20:390–400.
- REGASSA, R. 2013. Distribution, abundance and population status of Burchell's zebra (*Equus quagga*) in Yavello Wildlife Sanctuary, Southern Ethiopia. *Journal of Ecology and the Natural Environment* 5:40–49.
- REIF, U., AND H. KLINGEL. 1991. Hiding behaviour in wild gerenuk (*Litocranius walleri*) fawns. *Zeitschrift für Säugetierkunde* 56:159–168.
- RICHTER, J. 1970. Die fakultative Bipedie der Giraffengazelle *Litocranius walleri sclateri* Neumann 1899 (Mam. Bovidae), ein Beitrag zur funktionellen Morphologie. *Morphologisches Jahrbuch* 114:457–541.
- ROBINSON, T., AND N. OWEN-SMITH. 2004. How thermal conditions affect the activity patterns of African ungulates. *Advances in Ethology, Supplements to Ethology* 38:76.
- ROTHSCHILD, W. 1902. Appendix III. Mammals. Pp. 453–486 in *A sporting trip through Abyssinia* (P. H. G. Powell-Cotton, ed.). Rowland Ward, London, United Kingdom.
- RUSO, G. E. 2017. *Beatragus hunteri* (Artiodactyla: Bovidae). *Mammalian Species* 49:119–127.
- SAID, M. Y. 2003. *Multiscale perspectives of species richness in East Africa*. Ph.D. dissertation, University of Wageningen, Wageningen, The Netherlands.
- SCHERPNER, C. 1971. Architecture and display techniques. *International Zoo Yearbook* 11:57–62.

- SCHERPNER, C. 2011. Der Säugetierbestand (Arten und Tierzahl) des Zoologischen Gartens Frankfurt 1858 - 1993. Milu: Mitteilungen aus dem Tierpark Berlin-Friedrichsfelde 13:5–170.
- SCHOMBER, H. W. 1963. Beiträge zur Kenntnis der Giraffengazelle (*Litocranius walleri* Brooke, 1878). Säugetierkundliche Mitteilungen 11:1–44.
- SCLATER, P. L. 1884. On some mammals from Somali-land. Proceedings of the Zoological Society of London 1884:538–542.
- Slater, P. L., AND O. THOMAS (eds.). 1898. Genus *Lithocranius*. Pp. 227–237 in The book of antelopes, vol. III. R. H. Porter, London, United Kingdom.
- SIKES, S. K. 1967. Observations on the internal structure of the aorta in East African mammals, with particular reference to the klipspringer, gerenuk and hippopotamus. Zeitschrift für Säugetierkunde 33:27–42.
- SIKES, S. K. 1969. Habitat and cardiovascular disease: observations made on elephants (*Loxodonta africana*) and other free-living animals in East Africa. Transactions of the Zoological Society of London 32:1–104.
- SOKOLOV, V. E., O. F. CHERNOVA, AND FEKADU KASSAYE. 1994. The skin of some Ethiopian ungulates. PRIN Ltd., Moscow, Russia.
- SQUIRES, B., R. LOWRY, AND C. BANKS. 2016. Utilizing Zoos Victoria's Connect-Understand-Act model to enable social and biological gains in northern Kenya. International Zoo Yearbook 50:96–111.
- STICKLAND, N. C. 1979. Comparative aspects of muscle fibre size and succinic dehydrogenase distribution in the longissimus dorsi muscle of several species of East African mammals. Acta Anatomica (Basel) 105:381–385.
- THOMAS, O. 1891. On some antelopes collected in Somali-land by Mr. T. W. H. Clarke. Proceedings of the Zoological Society of London 1891:206–212.
- THOMAS, W. D., R. BARNES, M. CROTTY, AND M. JONES. 1986. An historical overview of selected rare ruminants in captivity. International Zoo Yearbook 24/25:77–99.
- TSCHOPP, R., ET AL. 2010. Bovine tuberculosis in Ethiopian wildlife. Journal of Wildlife Diseases 46:753–762.
- ULLRICH, W. 1963. Einige Beobachtungen an Wildtieren in Ostafrika. Der Zoologische Garten, NF 27:187–193.
- WALTHER, F. 1958. Zum Kampf- und Paarungsverhalten einiger Antilopen. Zeitschrift für Tierpsychologie 15:340–380.
- WALTHER, F. 1961. Zum Kampfverhalten des gerenuk (*Litocranius walleri*). Natur und Volk: Bericht der Senckenbergischen Naturforschenden Gesellschaft 91:313–321.
- WASSER, S. K., ET AL. 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. General and Comparative Endocrinology 120:260–275.
- WEIGL, R. 2005. Longevity of mammals in captivity; from the living collections of the world. Kleine Senckenberg-Reihe 48. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.
- WINKLER, H. A. 1939. Rock-drawings of southern Upper Egypt II, Sir Robert Mond Desert Expedition. The Egypt Exploration Society 27, London, United Kingdom.
- WOODROFFE, R., P. A. LINDSEY, S. S. ROMANACH, AND S. M. K. OLE RANAH. 2007. African wild dogs (*Lycaon pictus*) can subsist on small prey: implications for conservation. Journal of Mammalogy 88:181–193.
- WURSTER, D. H., AND K. BENIRSCHKE. 1968. Chromosome studies in the superfamily Bovoidea. Chromosoma (Berlin) 25:152–171.
- YOUNG, L. A., A. HOPKINS, S. CITINO, R. PAPENDICK, AND B. L. HOMER. 1994. Eastern equine encephalomyelitis in a gerenuk, (*Litocranius walleri*). Pp. 324 in Proceedings American Association of Zoo Veterinarians (R. E. Junge, ed.). Annual Conference 22–27 October 1994, Pittsburgh, Pennsylvania.
- ZOOTIERLISTE. 2019. A database for the current and former vertebrate inventories of European zoos and other public collections. www.zootierliste.de. Accessed 31 August 2019.

Associate Editor was SETH EISEB. Editor was MEREDITH J. HAMILTON.