

Giraffa camelopardalis. By Anne Innis Dagg

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Giraffa Brünnich, 1772

Giraffa Brünnich, 1772:36. Type species *Cervus camelopardalis* Linnaeus, 1758, by monotypy. *Giraffa* Brisson, 1762, although frequently cited, is in a work that is not consistently binomial and is therefore unavailable for purposes of nomenclature unless specifically validated by the International Commission on Zoological Nomenclature, a step that has not been taken, although some have advocated it.

Camelopardalis Schreber, 1784:pl. 255. Type species *Camelopardalis giraffa* Schreber, 1784, by monotypy.

Orasius Oken, 1816:744. Type species *Cervus camelopardalis* Linnaeus, 1758, by monotypy. Ruled unavailable, because in a work not consistently binomial, by the International Commission (Opinion 417, 1956, Bull. Zool. Nomenclature 14:1).

Trachelotherium Gistel, 1848:81. Proposed as a replacement name for *Camelopardalis* Schreber, 1784.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Giraffidae, Subfamily Giraffinae. There are only two living giraffids, the okapi, *Okapia johnstoni*, and the giraffe, *Giraffa camelopardalis*.

Giraffa camelopardalis Linnaeus, 1758

Cervus camelopardalis Linnaeus, 1758:66. Type locality "Sennar and Aethiopia."

Camelopardalis Giraffa Schreber, 1784:pl. 255 only, rather than Boddaert, 1785:133 as usually cited. Type locality of Schreber not given, Boddaert gave "Cape of Good Hope," but no giraffe have been found that far south; here restricted to Warmbad (as mapped in fig. 3), where Brink (1761) encountered and described giraffe just north of the Orange River.

Cameleopardalis antiquorum Jardine, 1835. Type locality "Sennar and Darfour," restricted to Baggar el Homer, Kordofan, about 10°N and 28°E by Harper (1940).

Camelopardalis aethiopica Ogilby, 1837:134. Type locality undesignated, by inference Ethiopia.

Camelopardalis capensis Lesson, 1842:168. Type locality Cape of Good Hope.

Giraffa senaariensis Trouessart, 1898:902. Type locality interpreted to be south of Sennar, Anglo-Egyptian Sudan by Allen (1939:468).

Giraffa tippelskirchi Matschie, 1898:78. Type locality Lake Eyassi, southeast of Victoria Nyanza, Tanganyika Territory (now Tanzania).

Giraffa schillingsi Matschie, 1898:79. Type locality Taveta, Kenya.

Giraffa infumata Noack, 1908:356. Type locality Barotse, middle Zambesi region, Northern Rhodesia (now Zambia).

Giraffa hagenbecki Knottnerus-Meyer, 1910:800. Type locality Gallaland, southern Abyssinia.

CONTEXT AND CONTENT. Context noted in generic summary above. Nine subspecies are recognized (Ansell, 1968) as follows:

G. c. camelopardalis (Linnaeus, 1758:66), see above (*biturigum* Duvernoy, *aethiopica* Ogilby, *typica* Bryden, and perhaps *congensis* Lydekker, are synonyms).

G. c. antiquorum (Jardine), 1835:187, see above (*senaariensis* Trouessart a synonym).

G. c. peralta Thomas, 1898:40. Type locality near Lokoja, at the junction of the Niger and Benue rivers in Nigeria, probably north of the confluence (Happold, 1969).

G. c. reticulata de Winton, 1899:212. Type locality the Loroghi Mts. in Kenya (*hagenbecki* Knottnerus-Meyer and *nigrescens* Lydekker are synonyms). Mertens (1968 a and b)

pointed out that *reticulata* de Winton, 1899, was a junior homonym of *reticulata* Weinland, 1863, but requested validation of de Winton's name and suppression of Weinland's by the International Commission on Zoological Nomenclature under their plenary powers, because Weinland's type locality was within the range of *antiquorum* rather than that of *reticulata* as these names have been used recently. The Commission has not yet (May 1970) acted on the request. The name *australis* Rhoads may also be a synonym.

G. c. rothschildi Lydekker, 1903:122. Type locality, as given originally, Uasin Gishu Plateau east of Lake Baringo, Kenya, corrected to west of Lake Baringo (Lydekker, 1908) (*cottoni* Lydekker a synonym).

G. c. tippelskirchi Matschie, 1898:78, see above (*schillingsi* Matschie a synonym).

G. c. thornicrofti Lydekker, 1911:484. Type locality Petauke, Eastern Province, Northern Rhodesia (now Zambia).

G. c. angolensis Lydekker, 1903:121. Type locality by the Cunene River 240 kms. southwest of Humbe, Angola (*infumata* Noack a synonym according to Ansell).

G. c. giraffa Schreber, 1784:pl. 255, see above (*capensis* Lesson, *australis* Swainson, *maculata* Weinland, and *wardi* Lydekker, are synonyms).

DIAGNOSIS AND GENERAL CHARACTERS. The genus is monospecific. Height is 5 to 6 m., females smaller than males; legs and neck each over 1.5 m. long. Slope of back makes forelegs appear longer than the hind legs, which they marginally are. Two unbranched permanent horns, in both sexes, are fused to the skull above the fronto-parietal suture and are covered with skin; a median "horn" anterior to this is more developed in males than in females; the facial region of the skull of old males is also covered with other irregular bony growths. Skull is up to 73 cm. long; molars brachydont, upper molars without inner accessory columns; canine teeth bilobed or trilobed. Hide has a buff color base on which are spread darker brown spots varying in shape from irregular jagged blotches to smooth polygons; spots large on body but small on head and upper legs. Tail is long and has long, black, coarse terminal hairs; neck maned with short, brown, stiff hairs.

DISTRIBUTION. Giraffe are widespread in Africa where there are scattered trees or bushes. Their range includes semi-arid regions but not deserts, rain forests, or mountain ranges. Within historic times their distribution has been much reduced, because of increasing aridity and increased human population pressures, and their numbers everywhere have declined because of hunting, farming and periodic epidemics of rinderpest. None now survive in North Africa but some may have remained in Morocco as late as A.D. 600 (Schomber and Kock, 1961:137). Recently, especially with the advent of drugging techniques, giraffe have been transplanted to areas of Africa (not shown in fig. 3) where they were not previously found, e.g. Orange Free State (Griesel, 1961), Natal, Swaziland

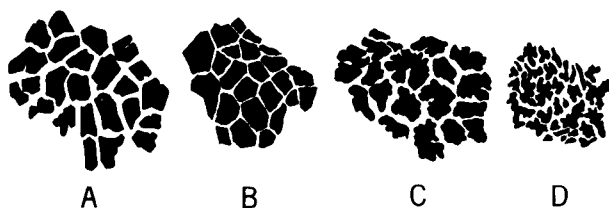


FIGURE 1. Patterns of trunk spots (all at about the same scale) of giraffe belonging to three adjacent subspecies (from Dagg, 1968): A, *G. c. rothschildi*; B, *G. c. reticulata*; C and D, *G. c. tippelskirchi*.

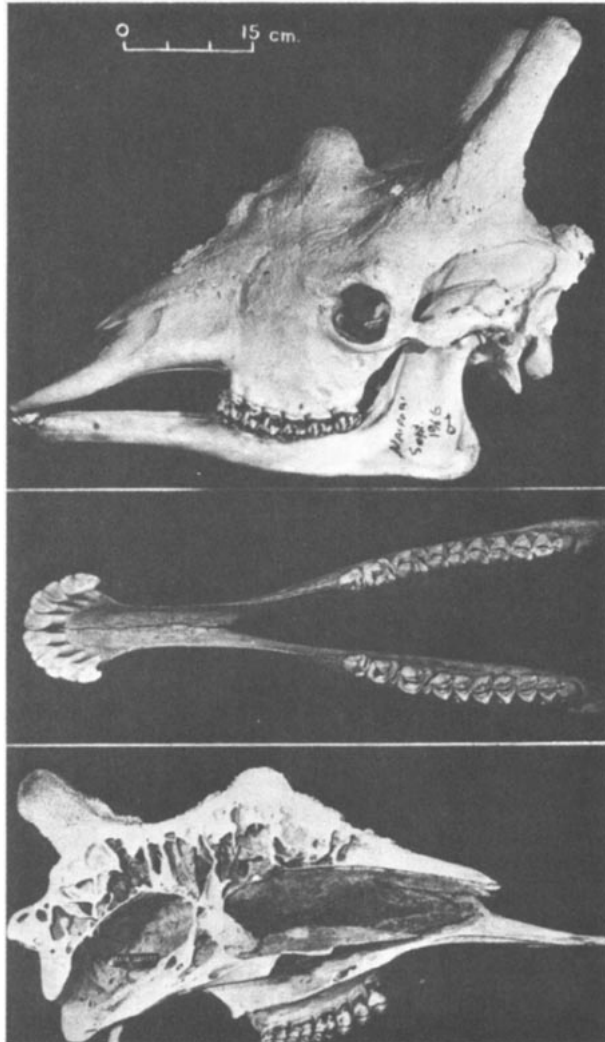


FIGURE 2. Top: Skull of adult male giraffe. Middle: Upper view of mandible (note the lobed canine teeth). Bottom: Section of skull of adult male showing extensive pneumatic sinuses. All photos by J. B. Foster.

(Kirk, 1966) and Saanane Island in Lake Victoria (Achard and McCulloch, 1967).

FOSSIL RECORD. The giraffids are believed to have evolved in the early or middle Miocene in central Asia (Churcher, 1970). Specimens thought to belong to *Giraffa camelopardalis* are known only from Pleistocene deposits of Israel and Africa itself. The Israeli records are for the lower Pleistocene of the central Jordan Valley (Haas, 1966) and for the Villafranchian at Bethlehem (Hooijer, 1958). The African records are for the Villafranchian from Tchad (Abadie *et al.*, 1959), for the middle Pleistocene of Olduvai, Tanzania (Hopwood, 1936) and for the lower Pleistocene from Omo, near Lake Rudolph (Arambourg, 1947). However, Leakey (1965) noted that the lower and middle Pleistocene specimens of *Giraffa* from Africa may not be of the species *G. camelopardalis*.

FORM. Lochte (1952) described five different types of hair found on giraffe. Broman (1938a) explored one of these types, from the mane, in detail. The mane, which is about 12 cm. long in the adult, can be identified microscopically in a fetus only 28 cm. long. The arrangement of hairs produces areas of hair whorls, feathering, and crests which seem to be correlated with positions or areas in which movement occurs in any particular region of the body (Kidd, 1900, 1903; Lankester, 1907; Rothschild and Neuville, 1911), although there is also much individual variation. The female has 4 mammae, Shortridge's (1934) widely quoted count of 2 mammae being an error. The milk of giraffe has been analyzed by Stephan (1925), Greed (1960), Ben Shaul (1962) and Aschaffenburg

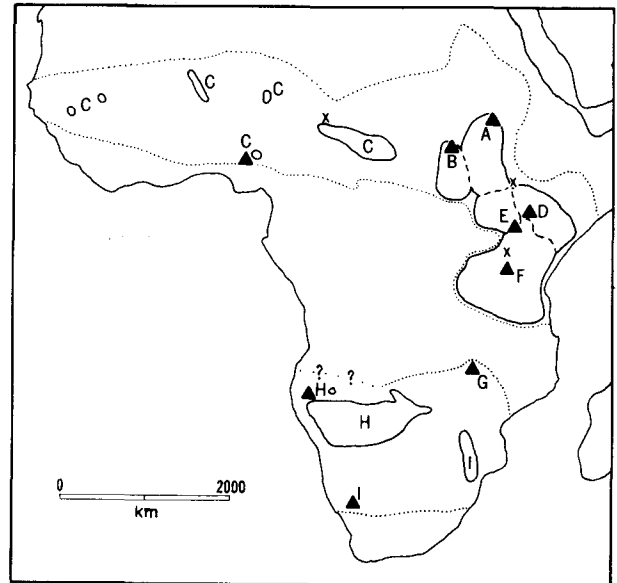


FIGURE 3. Recent distribution of the giraffe in subsaharan Africa, within historic times (outlined with dotted lines, after Krumbiegel, 1939), at present (outlined with solid lines), and at three fossil sites (marked X). Type localities of the nine recognized subspecies are shown by triangles: A, *G. c. camelopardalis*; B, *G. c. antiquorum*; C, *G. c. peralta*; D, *G. c. reticulata*; E, *G. c. rothschildi*; F, *G. c. tippelskirchi*; G, *G. c. thornicrofti*; H, *G. c. angolensis*; and I, *G. c. giraffa*.

et al. (1962). The teeth and bones of the giraffe are especially large but not otherwise greatly different from those of other pecoran species. The dental formula is $0/3, 0/1, 3/3, 3/3 = 32$. The molars are brachyodont and rugose. The row of front teeth is wide, in part because of the broad lobed canines, which makes the combing action used while browsing on leaves particularly effective. The skull has extensive air spaces, but, even with these spaces, its weight may reach 13 kg. in old males (Dagg, 1965). Dorsal neck muscles and ligaments attach to two enlarged bony areas at the back of the adult skull which are sometimes referred to as occipital, posterior, or mizzen horns (Thomas, 1901). The occipital condyles allow the head to be raised through an angle of more than 90° ; this allows free movement for browsing or fighting. The various sutures in the skull close at different times so that a skull of an animal up to at least six years of age can be aged fairly accurately (Singer and Boné, 1960). They also found that giraffe could be aged by sequences of eruption and wear of the teeth. The giraffe has only 7 cervical vertebrae, each very elongate, but the first of the 14 (rarely 13) thoracic vertebrae is modified to resemble a cervical vertebra too (Lankester, 1908). The dorsal spines of the anterior thoracics are long, forming the prominent hump on the upper back. They serve for the attachments of the large muscles and the nuchal ligament which support the neck and head. The thoracics are followed by 5 lumbar, 4 to 5 fused sacral and 16 to 20 caudal vertebrae. The pelvis is shorter than in most ruminants, and the upper ends of the ilia are more expanded (Flower, 1870). The legs are highly specialized; the first, second and fifth metapodials are usually absent. The joints and ligaments of the hind leg at least are very similar to those of antelope (Heinze, 1965). The hooves are low posteriorly so that the fetlock nearly touches the ground; this may increase the foot's ability to support a large weight. The footprint is about 31 by 23 cm. in an adult male and slightly less in a female. There are no interdigital glands or lateral hooves. The musculature of the giraffe has been broadly described by Owen (1841), Joly and Lavocat (1843) and Murie (1872). More recently, smaller muscle groups have been studied in depth: the neck and shoulder muscles by Chaine (1902), Rothschild and Neuville (1911), Zuckerman and Kiss (1932), Willemse (1958) and Angermeyer (1966); the foreleg muscles by Bego (1960); and the hind leg muscles by Heinze (1964, 1965). The circulatory system is specialized to cope with the high blood pressure necessary in the giraffe to pump blood to the brain. The arteries of the neck have thick walls composed largely of elastic tissue al-

though in the carotids the muscle fibres increase in prominence towards the head (Franklin and Haynes, 1927). The blood pressure at the brain is regulated by a *rete mirabile* into which the external carotids divide (Lawrence and Rewell, 1948). The blood pressure in the carotid may reach 353 (systolic) to 303 (diastolic) mm. Hg. in an experimental animal (Goetz and Keen, 1957; Goetz *et al.*, 1960). Some large veins are extensively valved, to help counteract the effects of gravity (Amoroso *et al.*, 1947). The veins of the legs are very thick and muscular and have tiny lumens. In general, the vessels from various parts of the body have wide variations in structure corresponding to the prevailing hydrostatic pressure (Goetz and Budtz-Olsen, 1955; Goetz and Keen, 1957; Goetz *et al.*, 1960). The heart of a wild female weighed 12 kg. (Goetz and Budtz-Olsen, 1955), far more than those of captive giraffe. The wall of her left ventricle was 7.5 cm. thick. The atrioventricular node is large in the giraffe and the Purkinje cells and fibres are particularly well developed (Castigli and Sacchi, 1941). A heart bone up to 2.5 cm. long is present in adults (Crisp, 1864b). There are twice as many blood cells per cubic mm. in the giraffe as in man, but otherwise the blood is not particularly distinctive (Goetz and Budtz-Olsen, 1955). Nor did these men find the fetal circulation especially noteworthy. The spleen is not unlike that of other ruminants (Crisp, 1853; Lönnberg, 1900; Retterer and Neuville, 1916; and Derscheid and Neuville, 1925). The brain of the giraffe is relatively small compared to the size of the animal, the weight ratio is about 1:800, which is similar to that of the horse. The anatomy of the brain is detailed by Black (1915), Friant (1952, 1954) and Kato (1963). The total length of the nerves is immense in the giraffe, but their arrangement is much as in other ungulates. Because the trachea of the giraffe is so long, the giraffe has a large respiratory dead space where no exchange of gases can take place. This is partly balanced by a large total lung capacity. Patterson *et al.* (1957) calculated that the resting tidal volume of the giraffe is about 4 liters per breath and that these animals, like men, use about $\frac{1}{10}$ to $\frac{1}{12}$ of their total lung capacity under basal conditions. A giraffe breathes only about 8 to 10 times a minute (Robin *et al.*, 1960). The vocal cords are of the simple form present in most ruminants (Burne, 1917). They enable giraffe to make a variety of sounds although they seldom do so. The digestive system is complex in the giraffe, which eats only leaves and twigs. The prehensile lips are extensively haired as a protection against thorns. The dark-coloured tongue is up to 54 cm. long (Schneider, 1951) which increases the reach of the animal appreciably. Both it and the inside of the mouth are extensively covered with papillae (Sonntag, 1922). The salivary glands are large as in all ruminants but the palatine tonsils are small (Burne, 1917; Hett, 1928). The long muscular oesophagus leads to the rumen, the first of the four stomach compartments which are all modified for the diet of a "selective feeder" (Hofmann, 1968). In the rumen the food is thoroughly moistened by gastric juices and partly fermented before being shaped into boluses that are rechewed as the animal ruminates. There are no special stomach cells for water retention (Fox, 1938). The intestines of an adult are about 80 m. long. Beyond the ileo-caecal junction there are various crypts that increase the surface where mucous is secreted (Neuville, 1922). The caecum itself is large. The feces are eliminated from the anus as acorn-like pellets about 4 cm. long. The liver shows few signs of lobulation (Neuville, 1914). The hepatic ducts unite to form a long common bile duct which opens in the duodenum about 30 cm. beyond the pylorus (Cave, 1950). A gall bladder may or may not be present; Cave (1950) found only 2 in 19 dissections of giraffe but Kobara and Kamiya (1965) found one in each of 2 female adults they examined. The kidneys were described by Wrobel (1965). The reproductive systems resemble those of other ungulates. The placenta is typically polycotyledonary, with large, many-branched villi (Mossman, 1937; Ludwig, 1962). Wilkinson and de Fremery (1940) detected gonadotropic hormones in the urine of a pregnant female. The giraffe lacks preorbital, inguinal and interdigital glands (Pocock, 1910). The pituitary is quite large, especially the adenohypophysis (Hanström, 1953; Kladetzky, 1954). Frank (1960) discussed the parathyroid and thyroid glands of the giraffe.

FUNCTION. Few physiological experiments have been carried out on giraffe except on the circulatory system. To study this, wild giraffe have been drugged so that apparatus could be fastened to individuals to determine their blood pressures. The maximum blood pressure in the carotid artery at the base of the brain in a female surrounded by scaffolding

was 200 mm. Hg. when she was standing but only 175 mm. Hg. when she lowered her head (Goetz and Budtz-Olsen, 1955). The mechanism that controlled the blood pressure so effectively was not related to a high viscosity or high protein content of the blood, as these values in the female giraffe were not unlike those in man. Recently information has been obtained via radiotelemetry in free-ranging giraffe (Van Citters *et al.*, 1966). An animal while resting had a low blood pressure reading from the carotid artery of 150 (systolic) to 105 (diastolic) mm. Hg. When galloping, these values increased to 230/125 mm. Hg. The pulse rates ranged from 60 to 170 beats per minute. The blood flow in the carotid artery ranged between 50 cm.³/sec. in a prone giraffe and 35 cm.³/sec. in a standing one. The peak systolic blood velocity was 60 cm./sec.; during diastole the velocity fell to nearly 40 cm./sec. (Van Citters *et al.*, 1968). Radiotelemetric thermometry has been used to determine the deep body temperature of a giraffe (Bligh and Harthoorn, 1965). At low ambient temperatures the deep body temperature in the lower neck of a 400 kg. female was remarkably thermostable at between 37.75°C and 39.1°C. This thermostability may be relaxed at high ambient temperatures, as in eland *Taurotragus oryx* (Taylor and Lyman, 1967), and this would help the giraffe keep cool while conserving water. Backhaus (1959) studied color vision in a captive giraffe. He offered food in variously colored containers and judged that the animal could distinguish between red, orange, yellow, yellow-green and violet.

ONTOGENY AND REPRODUCTION. Following copulation the fertilized egg implants without delay. The gestation period averages 15 months (the mean of 35 pregnancies of captive females, Backhaus, 1961), but varies considerably, from 394 days for a small animal that died shortly after birth (Lang, 1955) to 488 days (Robinson *et al.*, 1965). In two male fetuses, 28 cm. in body length and about 3 months of age, no hair was visible macroscopically (Broman, 1938b), the main horns were indicated by two mounds above the skull 8 mm. in diameter and 5 mm. high, and the testes had already descended into the scrotal sacs. In a female fetus, 60 cm. long and about 4 months old, also described by Broman, hairs were evident on various parts of the head, especially on both lips and on the upper eyelid, and on the tip of the tail. The main horn *anlagen* were 2 cm. in diameter and 5 mm. high while the anterior horn was represented as a minute bump. The incisors and canines were visible through the gums. The 4 teats were papillae 3 to 4 mm. high and 1.5 mm. thick. Beddard (1906) noted in an 8 month fully haired fetus that the hairs were all whitish so that there were no spots. The horn cartilages could be felt through the skin above the skull. The hooves were soft and quite pointed. Many parturitions have been observed in captivity. The forelegs and head of the young appear first, after the rupture of the fetal membranes. The young is slowly pushed outward as the mother strains while standing with her hind legs spread apart. The umbilical cord breaks about 30 cm. from the abdomen as the young falls to the ground (Gijzen, 1958) and at this time the animal first begins to breathe (Harrison Matthews in Slijper, 1958). The process lasts from 20 minutes to several hours (Gijzen, 1958). Only one young is born at a time. The only sure record for twinning is from the San Francisco Zoo where two stillborn twins, together weighing only 41 kg., were born in 1943 (Reuther, pers. comm.). Backhaus (1961) recorded the dates of calving of 53 females in captivity and found that these occurred throughout the year. Giraffe also breed throughout the year in the wild, although different seasonal peaks in different areas and in different years for the same area have been noted—in the Kruger National Park from October to January (Stevenson-Hamilton, 1947), from February to April (Brynard and Pienaar, 1960), for September and October (Pienaar, 1963) and for February to March and August to October (Fairall, 1968). Ansell (1960) found no definite calving seasons for giraffe in Zambia, although he states that October and March have been mentioned by other authors. In Rhodesia, Dasmann and Mossman (1962) reported that most births occurred in May during the dry season. In the Nairobi National Park and Serengeti Park most young were also born during the dry months (J. B. Foster and G. Schaller, pers. comm.), although parturitions occurred near Nairobi in every month. In captivity 78% of 27 calvings took place in the daytime, but these times may have been influenced by the presence of human observers (Backhaus, 1961). The neonate is about 2 m. tall at birth and weighs about 54.5 kg. (mean of 16 captive neonates). It has a relatively shorter neck than the adult which it holds in a more erect position. Its spots tend to be paler than those of older animals. The hair

is short and slightly woolly. The horn cartilages lie flat at first under the skin but become upright between two hours (Benchley, 1946) and four weeks (Sigel, 1886) after birth and fuse to the skull during ossification. Their position is indicated by two prominent tufts of black hair. In the Nairobi National Park the male to female ratio of newborn calves was 31:30 (Foster, pers. comm.) but Bourlière (1961) found that of 117 captive neonates 61.5% were males. Calves can stand and suck at 10 minutes after birth, and walk and run soon afterwards (Gijzen, 1958). They can look after themselves within a few months. They supplement their milk diet with leaves after a few weeks although they may suck for over a year. In captivity even adults will suck, although the mother will not allow them to do so unless her own calf is already sucking (Dagg, 1970). The young grow at least 1 m. during their first year and approach their full size at 4, although they may continue to grow slightly until they are 7 or 8 years old (Owen, 1841; Paulus, 1943; Reventlow, 1949). At this time a wild female stands about 4.3 m. and a wild male about 5.3 m. Captive giraffe seldom exceed 5.0 m. with a shoulder height in males of about 3.3 m. The average adult weight is considered to be 800 kg. (Stewart and Zaphiro, 1963) although a large male may weigh 1220 kg. or more (Crile, 1941). The females become sexually mature at 3½ years and the males at about 4½ years of age (Gijzen, 1958). The female thereafter comes into heat about every 14 days (Lang, 1955) and can conceive while she is lactating. She can breed until she is at least 20 years old (Ried, 1958). A captive male that had sired many giraffe was no longer breeding at 24 years of age (Dagg, 1970). In captivity the oldest giraffe attained 28 years of age (King, 1947) but giraffe in the wild not uncommonly live at least up to 26 years (Foster, pers. comm.). The mortality of adult giraffe is not great in the wild, but in their first year of life as many as 68% of those born may die (Foster, pers. comm.).

ECOLOGY. Lions are by far the major predators of giraffe (Wright, 1960; Brynard and Pienaar, 1960; Pienaar, 1963; Kruuk and Turner, 1967) although on rare occasions a lion itself may be killed by a giraffe (R. Douglas of Tanganyika Safaris, Arusha, pers. comm.; Campbell, 1951). Cheetah and crocodiles kill giraffe very rarely—0.28% each of 675 giraffe kills in the Kruger National Park over a 25 year period (Pienaar, 1969). The other kills were all by lion. Various tickbirds live commensally with giraffe—the buffalo weaver *Texor niger* (FitzSimons, 1920) and the red-billed and yellow-billed ox-peckers *Buphagus erythrorhynchus* and *B. africanus* (Attwell, 1966). These birds call out at the approach of a man and probably of other predators too (Attwell, 1966). They also serve a giraffe by searching through its hair for ticks, which they eat. They sometimes peck at wounds, so aggravating them, but perhaps they compensate for this by devouring maggots in the area.

Ticks usually infest giraffe, particularly on the relatively thin-skinned area of the genitalia. The common species include the bont tick *Amblyomma hebraeum*, blue tick *Boophilus decoloratus*, brown tick *Rhipicephalus appendiculatus* (Innis, 1958), *Rhipicephalus camelopardalis* (Walker and Wiley, 1959) and *Hyalomma aegyptium* (Lönnberg, 1912). On giraffe imported into New York the following ticks were found: *Amblyomma gemma*, *Boophilus decoloratus*, *Hyalomma albiparmatum* and *Rhipicephalus pulchellus* (Becklund, 1968). Internal parasites are more numerous. Species that have been identified are *Cooperia pectinata*, *C. punctata*, *Haemonchus contortus*, *H. mitchelli*, *Trichuris globulosa* (Ortlepp, S. Afr. gov't., pers. comm.), *Trichuris giraffae*, *Parabronema skrjabini*, *Monodontella giraffae* (Leiper, 1935), *Trichocephalus gracilis* (Cobbold, 1860), *Uncinaria smithi* (Weidman, 1918), *Haemonchus* sp., *Trichostrongylus* sp. (Sloan, 1965), *Fasciola gigantica* (Cobbold, 1855), *Taenia saginata* = *Cysticercus bovis* of Schwartz, 1928, *Moniezia nullicollis* (Yamaguti, 1959), *Echinococcus* sp. (Crisp, 1864a) and *Rhinoestrus* sp. (Laurence, 1961). Dinnik and Sachs (1968) found protostrongylid larvae in the droppings of wild giraffe in Tanzania.

Giraffe have little competition for food, since the tallest bovid cannot browse above a height of 2.5 m. Even when the giraffe browses on low bushes it often chooses one with many thorns that other ruminants avoid. By far the best data for population structure and dynamics of giraffe have been collected by Foster (1966 and pers. comm.) from the approximately 80 giraffe of the Nairobi National Park. Apparently the population increases by nearly 25% each year but of these young about 68% die in their first year. The young often wander away from their mothers at an early age but these young do not have a greater mortality than the young that re-

main near their mothers. In 1967 the resident giraffe population of the Nairobi National Park was estimated at 31% adult female, 25% adult male, 12% in their fourth and fifth years, 8% in their third year, 10% in their second year and 14% in their first year. These percentages have been quite stable for seven years. The average life span of a giraffe was about six years, but some lived more than 25 years. In Wankie and Garamba National Parks, Dasmann (pers. comm.) and Backhaus (1961) respectively estimated about 30% of the giraffe were immature and 20% of these were calves. In South Africa, Innis found only 12% of the giraffe were immature and half of these were calves. The proportion of females was low in this population. Giraffe are usually found on lightly forested areas, always near trees or bushes. They are often sedentary animals, seldom moving great distances except when forced to by fire or drought (Innis, 1958). In Nairobi National Park, Foster (pers. comm.) found that the bulls were more restless than the cows, often walking from herd to herd presumably to find a female in heat. One male was spotted 50 km. from the Park. The giraffe in the Park are not all permanently established, because although there are about 80 giraffe there at one time, these may be any of 241 individuals. Giraffe do not show territorial behavior. In the Nairobi National Park, Foster (pers. comm.) calculated the average home ranges for the 10 most commonly seen males and females at 62 and 85 sq. km. respectively.

Various diseases have been reported in wild giraffe, the most virulent of which is rinderpest. This disease first swept through Africa in the 1890's, killing hundreds of giraffe and other ruminants (Grzimek, 1956a). There have been scattered outbreaks in Africa since then, including a severe epidemic in northern Kenya in 1960 where about 40% of the giraffe died (Simon, 1962). Earlier in this same area an epidemic of gastroenteritis killed some giraffe (Percival, 1924) and others died during a brief outbreak of anthrax in southern Africa (Pienaar, 1961). This disease was suppressed by disinfecting the water sources responsible for the spread of the infection (Payne, 1961). Giraffe eat from a variety of species of plants, many of them acacias. Lists of species eaten are given by Innis (1958), Van der Schijff (1959), Brynard and Pienaar (1960), and Foster (1966). Giraffe eat the leaves, but sometimes also the pods, fruit and twigs of these trees and bushes. They are not deterred by the presence of long thorns and spines on their food plants but they may be by ants (Brown, 1960). Throughout most of Africa at present, the giraffe is a protected species although a few may be shot on special licenses for museums or sport. Undoubtedly a number are also poached each year. Giraffe are found in zoos throughout the world, where they breed readily. Some captive mothers refuse to suckle their young, but these calves can be raised using bottled milk (Zellmer, 1960; Savoy, 1966). The Africans have always used parts of giraffe—the flesh for meat; the skin for shields, sandals and drums; the tendons for stringed musical instruments and thread; and the tail hairs for bracelets, flyswitches and thread. With the coming of the white man many more giraffe were killed and the species eliminated in areas where it conflicted with man. Now it is fully protected in many national parks. Giraffe were formerly captured in stockades (Ogrizek, 1954; Stanton, 1955) or by lassoes (Webb, 1954) but now they are usually drugged by darts (Pienaar *et al.*, 1966). Drugs and tranquilizers were used in the circulation experiments discussed earlier. They have also been used to allow Foster (pers. comm.) to put a radio transmitter collar onto a giraffe to study home range. In most of his work, Foster has identified individuals by photographing the left side of each animal's neck. The arrangements of the spots are unique in each individual, so that it can always be identified once photographed.

BEHAVIOR. Dagg (1970) has studied tactile encounters between individuals in a herd of 18 captive giraffe. The two sexually-active males were the most active in initiating such encounters, and the four calves the least active. Nosing and licking were the most common types (53% together of the 1590 encounters), followed by rubbing and hitting (18% and 14%). Sniffing genitalia and "urine testing" were infrequent and usually done by a bull to a cow. Necking matches were rare and always involved a male and a female although in the wild they are restricted to males (Coe, 1967). These types of behavior are apparently not seasonal, either in captivity or in the wild. Mating was observed twice and was similar to mating in the wild (Innis, 1958), with the male following a receptive female and mounting her when she stood still a number of times over a several hour period. The giraffe were all tolerant of each other generally, the dominant male sometimes allowing the

second male to make sexual advances to a female in heat. During the day most giraffe fed in early morning and in the late afternoon, although some at least also browsed after dark (Innis, 1958). In the wild they spent more time hunting for food during the dry season than during the growing season, and less time resting and cuddling (Innis, 1958). Giraffe communicate indirectly with other giraffe and other species by either standing motionless and staring at possible danger or stampeding from it. Either reaction sooner or later attracts the attention of other animals. Giraffe can communicate by vocal noises, but they do so rarely. Occasionally a giraffe will grunt when alarmed, annoyed, or hungry and a female and her calf may call to each other with a moo or low. Giraffe do not move far, generally. In South Africa, browsing giraffe averaged 0.21 km./hr. (Innis, 1958). Giraffe have only two gaits: walking and galloping at speeds up to 56 km./hr. (Arbuthnot, 1954). These have been analysed by Dagg and De Vos (1968a and b) and Bourdelle (1934) and compared with the gaits of other pecoran species. The walk of the giraffe is notable because an individual swings the two legs on one side of its body forward almost in unison. The long legs, relatively short trunk and large inertia of the body influenced the evolution of this gait. The movement of the long, heavy neck of the giraffe is correlated with that of the legs. This is particularly true in the gallop and in the jumping of fences (Dagg, 1962 b and d). The neck is also used to express various emotions in the giraffe (Backhaus, 1961). In the standing animal the angle of the neck to the ground is about 50° to 60° in adults and to 70° in calves. If it wants to threaten another giraffe or a person, it lowers its neck and head until they are nearly horizontal with the ground. It may begin a sparring match this way. If one giraffe submits to a stronger one it holds its neck high with its nose pointing upward. If it is alert or nervous, it holds its head more nearly perpendicular than usual, with its mouth pointing to the ground and its nostrils open wide. If it is preparing to flee it turns its body at an angle to the disturbance. When it shakes its head, it holds its neck about 45° from the horizontal. There is no evidence that giraffe are more intelligent than other ruminants, but they can learn to beg for food in captivity, to recognize human beings and to answer to their names. The chief activity of the giraffe is browsing, at times they stretch up as high as they can reach for leaves and at other times they bend low over a thorn bush. They often drink regularly at dams, rivers, or cattle troughs but they can apparently go for long periods without water too (Mason, 1937; Vesey-Fitzgerald, 1960). They approach water cautiously, frequently raising their heads several times between drinks. They can swallow with their heads at ground level however. In general, giraffe exhibit offensive behavior intraspecifically by hitting other giraffe with their horns and heads, and defensive behavior interspecifically by kicking out at predators with their hooves. Giraffe sleep deeply perhaps 20 minutes a night, folding their necks along beside their lying bodies to do so. Calves sleep for up to an hour (Grzimek, 1956b; Immelmann, 1958; Hediger, 1959; Backhaus, 1961; Immelmann and Gebbing, 1962). They rest for much longer periods, sometimes during the middle of the day. During such rest they often ruminate, chewing each bolus for about a minute before swallowing it and regurgitating the next. They rest either while standing, when their necks may bow down slowly toward the ground, or while lying. They lie down by bending first their front and then their hind legs. They get up again by resting first on their front "knees," then on their hind feet and then on their front feet (Dagg, 1962b; Zannier-Tanner, 1965). Occasionally giraffe, especially calves, will run about for no apparent reason, but there is no more highly organized play. A grooming animal licks itself with its tongue or bites its hide with its mouth (Backhaus, 1961). It may also rub itself against bushes to relieve itching in the skin. Flies are kept away in part by swishes of the giraffe's tail.

GENETICS. Wallace and Fairall (1965) have analyzed chromosomes of a male and a female giraffe, both drugged, from Kruger National Park. The modal number of chromosomes per cell was 30. The 28 paired autosomes were mainly metacentric and submetacentric with one pair of acrocentric chromosomes which were small. The large X chromosomes were submetacentric and the small Y chromosome metacentric. Little work has been done on phenotypic genetics in giraffe, although spotting intermediate in appearance between that of two races has been noted where such races are adjacent (Stott, 1959; Knottnerus-Meyer, 1910; Lydekker, 1911; Dagg, 1962c; Anon., 1910). Krumbiegel (1951) and Dagg (1968) described such racial hybridizations in captivity. Dagg con-

cluded that the number, area and shape of the spots on an animal are inherited, but not in the simple manner suggested by Spinage (1968). She also concluded that horn development is not under close genetic control, despite the emphasis on the horns in many early taxonomic studies.

REMARKS. Not all of the works cited were seen by the author.

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