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Cephalophus maxwellii.

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Cephalophus maxwellii (H. Smith, 1827)

Maxwell's Duiker

A[*ntilope*] *maxwellii* H. Smith, 1827:347. Type locality Sierra Leone.
A[*ntilope*] *philantomba* H. Smith, 1827:349. Type locality Sierra Leone.
Ant[*ilope*] *frederici* Laurillard, 1842:623. Type locality Senegal.
Cephalophus punctulatus Gray, 1846:167 (not Gray, 1850: 125). Type locality Sierra Leone.
Cephalophus whitfieldii Gray, 1850:12. Type locality Gambia.
Cephalophus liberiensis Hinton, 1920:530. Type locality Mt. Barclay, Liberia.
Cephalophus danei Hinton, 1920:531. Type locality Yatward Island, Rokelle River, Sierra Leone.
Cephalophus lowei Hinton, 1920:531. Type locality Tasso Island, Rokelle River, Sierra Leone.

Synonymy adapted from Lydekker and Blaine (1914).

CONTEXT AND CONTENT. Order Artiodactyla, Family Bovidae, Subfamily Cephalophinae. The genus *Cephalophus* contains 12 species (Ansell, 1968), 13 species (Heyden, 1969), or 14 species (Haltenorth, 1963). Three subspecies of *C. maxwellii* are recognized (Haltenorth, 1963; Ansell, 1968) as follows:

C. m. maxwellii (H. Smith, 1827:344), see above (*philantomba* H. Smith, *frederici* Laurillard, *whitfieldi* Gray, and *punctulatus* Gray are synonyms).
C. m. lowei Hinton, 1920:531, see above (*danei* Hinton a synonym).
C. m. liberiensis Hinton, 1920:530, see above.

The validity of these subspecies is in some doubt. Hinton had only a few specimens. Dekeyser (1956) thought that *lowei* and *liberiensis* were synonyms. Hayman (1935) and Ansell (1968) suggested that adequate material might show clinal variation, presumably with size increasing and incidence of horns in females decreasing from west to east.

DIAGNOSIS. The species most likely to be confused with *C. maxwellii* is *C. monticola*. Most authors distinguish these two on the basis of pedal gland structure (Ansell, 1968). The pedal gland is in a subcircular sac at the end of a narrow canal in *C. maxwellii* (Pocock, 1910), whereas in *C. monticola* the pedal gland is in a simple orifice (Pocock, 1910; Ansell, 1960—see figure 1). Heyden (1969) measured 60 skulls of *C. monticola* and 27 skulls of *C. maxwellii*. The greatest basal length (from ventral rim of foramen magnum to tip of premaxilla) was 116.5 mm in *C. monticola*, whereas the shortest basal length for *C. maxwellii* was 116.9 mm. He concluded that, although occasional overlap may occur, *C. monticola* can be distinguished by its smaller skull and narrower nasal region. The mean width at the suture between the premaxilla and the maxilla (measured on the ventral surface) in *C. maxwellii* skulls was 18.3 mm, whereas the mean for this measurement in *C. monticola* skulls was only 13.3 mm. Because of the great intraspecific variability in coat color in the two species, they cannot be separated on the basis of this character (Heyden, 1969). Some consider the two to form a superspecies (Ansell, 1968; Heyden, 1969); others lump them into a single species (Dorst and Dandelot, 1970). In view of the great similarity of *C. maxwellii* and *C. monticola* and the scarcity of knowledge about them, information on some aspects of the biology of *C. monticola* has been included in the present account to fill gaps where the corresponding information for *C. maxwellii* was lacking.

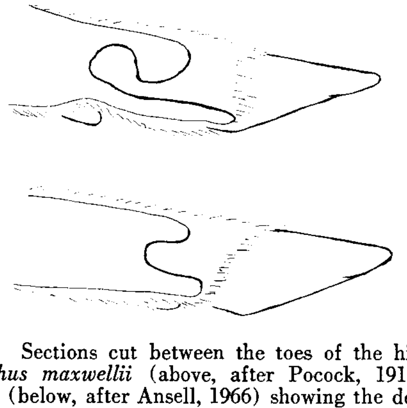

FIGURE 1. Sections cut between the toes of the hind feet of *Cephalophus maxwellii* (above, after Pocock, 1910) and *C. monticola* (below, after Ansell, 1966) showing the deeper pedal gland of *C. maxwellii.*

GENERAL CHARACTERS. This small antelope has a convex back, higher at rump than at shoulders. Head is relatively small with crest of longer hair between and around horns, ears are relatively short and rounded, and muzzle is naked (figure 2). Horns of male are short, conical, straight, ribbed at base, and in same plane as dorsal surface of skull. Horns are present or absent in female. Skull is broad and stout with relatively narrow muzzle and large lacrimal depressions (figure 3). Heyden (1969) gave a mean basal length of 126.6 mm and mean greatest width of 64.5 mm for 27 skulls. Maxillary (preorbital) glands are well developed, inguinal glands lacking, pedal glands present. Hoofs on lateral toes are small. Four inguinal mammae are present. Coat is gray-brown to blue-gray with great individual variation, even in animals caught at the same locality (Aeschlimann, 1963). A paler superciliary streak extends to base of horns. No mane present on shoulders. Underparts are whitish. Tail is darker with a white border, the distal half somewhat bushy. Average size and weight are greater in females than in males. For detailed description see Haltenorth (1963) who gave the following measurements: total length 63 to 100 cm, body length 55 to 90, tail 8 to 10, height 35 to 38, horns of male 3.5 to 6, weight 8 to 10 kg. For photographs of living specimens see Aeschlimann (1963), Ralls (1970, 1971*a*), and Walker (1964).

DISTRIBUTION. Ranges through the lowland forest zone and adjacent gallery forest from the lower Niger west to Gambia and adjacent Senegal (figure 4). Occurrence in the

FIGURE 2. Photograph by William Meng of an adult male *Cephalophus maxwellii* at the New York Zoological Society.

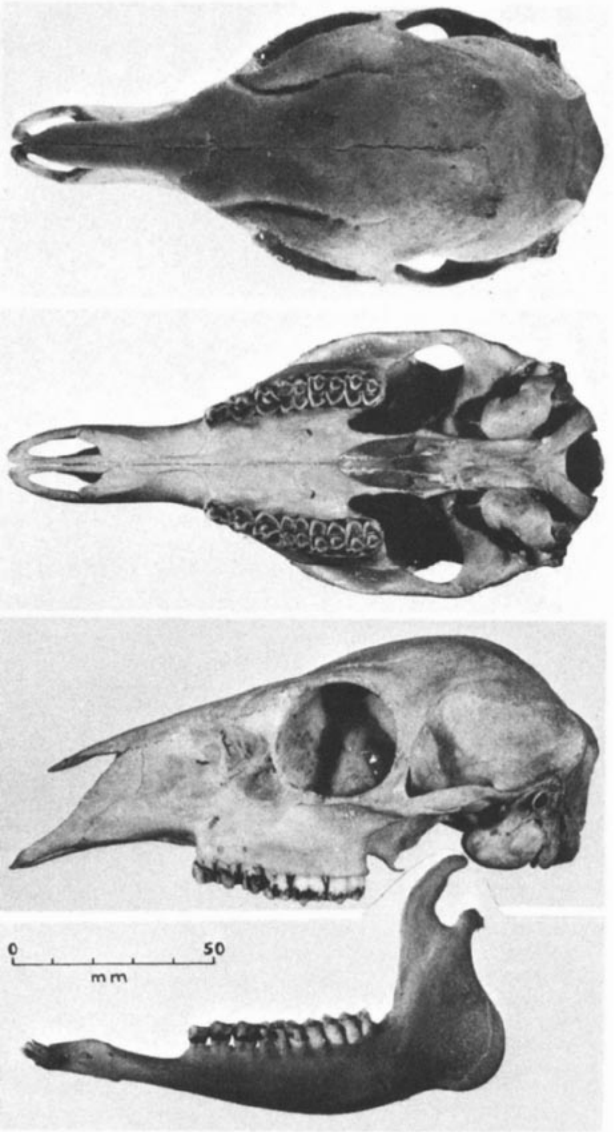

FIGURE 3. Photographs of the skull of a female (Museum of Comparative Zoology, Harvard University, no. 42715) from the former Gold Coast, shown (from top down) in dorsal, ventral, and lateral views. Photography by R. E. Logan, Department of Photography, American Museum of Natural History.

Cameroun area is uncertain. Aside from a possible small overlap in the Cameroun area, *maxwellii* and *monticola* are allopatric and may be regarded as a superspecies (Ansell, 1968). Heyden (1969) regarded the Niger River as the boundary between the two species, *maxwellii* occurring to the west and *monticola* to the east and south. He reached this conclusion after mapping the sites where both species have been collected over a period of 70 years.

FOSSIL RECORD. The earliest fossil referred to *Cephalophus* is a third molar from the Miocene of North Africa (Arambourg, 1959). *Cephalophus* also has been reported from the Pliocene of North Africa (Heyden, 1969). Two fossil species are known from the early Pleistocene of South Africa—*C. pricei* Wells and Cooke, 1957, and *C. parvus* Broom, 1934. *C. pricei* has features reminiscent of both *Cephalophus* and *Sylvicapra* in its teeth but Wells and Cooke placed it in the former because of the shape of the horns. The *C. parvus* specimen consists only of a broken piece of the mandible with two teeth; Broom thought it was closely related to *C. monticola*. The Cephalophinae are believed to have separated from the other Bovidae rather early, perhaps in the early Miocene, and to have remained primitive in many respects (Thenius and Hofer, 1960).

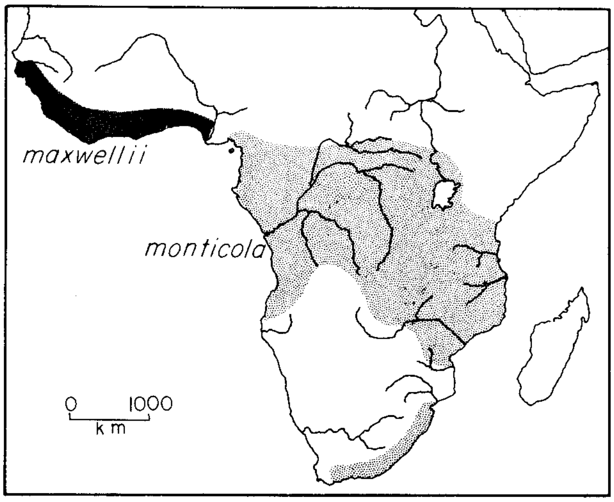

FIGURE 4. Ranges of *Cephalophus maxwellii* and *C. monticola* in Africa, based on collections over a 70-year period and adapted from Heyden (1969:395).

FORM. The rhinarium is pictured in Pocock (1918). The preorbital glands of the Cephalophinae differ in structure from those of all other artiodactyls. Weber (1888) suggested that they be given the name "maxillary glands" and Schaffer (1940) also used this terminology. The gross morphology of these glands in *C. maxwellii* was described by Pocock (1910). They are conspicuous in the living animal as a large swelling below and in front of each eye (Ralls, 1971a). The swelling is surmounted by a naked, concave arc of skin roughly 25 mm in length, studded with a row of about 25 pores from which the secretion emerges if the gland is pressed. For histological details, see Weber (1888) and Schaffer (1940). The skull of the Cephalophinae is characterized by a large lacrimal fossa, formed in part by the nasal, which accommodates this gland. For detailed description of the skull and tables of cranial measurements, see Heyden (1969). Lehmann (1961) described a cartilaginous "tooth" behind the canine of *C. monticola*. The primitive chewing musculature of *C. monticola* was described by Krapp (1969). Duikers have large hearts, the relative weight being approximately double that of the human heart (Hofmann and Scholz, 1968). Friant (1939) illustrated the external surface of the cerebral hemispheres in *C. maxwellii*. According to Oboussier (1966), the gyral pattern is similar in all the Cephalophinae and resembles that of cervids. The liver is small and simple. A gall bladder is lacking (Garrod, 1877, Pocock, 1918). The spleen is relatively small and covers only a small region on the left dorso-lateral aspect of the rumen (Hofmann and Scholz, 1968). The penis was pictured by Garrod (1877).

FUNCTION. According to Hofmann (1968) the duiker stomach has the morphological characteristics associated with the habit of feeding selectively on plants or parts of plants with presumably high nutritional value. These include a smaller rumen than that of roughage eaters, a relatively big reticulum, a small, flat, and kidney-shaped omasum, and a relatively small abomasum. The lesser capacity of the rumino-reticulum may be compensated for by the greater absorbing area of mucous membrane found in this type of stomach. Hofmann and Scholz (1968) distinguished three major types of ruminant body shapes, functionally related to habitat and flight behavior. Duikers have a "Type C" body shape, with a convex back with a high point in the lumbar region. The head is frequently lowered or stretched forward. This type is characteristic of animals of the dense bush and forest into which they "submerge" with one or two jumps.

ONTOGENY AND REPRODUCTION. The following information is from Aeschlimann (1963). In the Ivory Coast, calves are born mainly during the two dry seasons, January to March and August to September. Females can produce a calf each year. Only one is born at a time, after a gestation period of 120 days. It resembles its parents in color, unlike the calves of some duikers, and weighs from 710 to 954 gm, or roughly one-tenth the weight of the adult female. Individuals may survive in captivity for up to 10 years.

ECOLOGY. This species of the forest floor is found both in the thick underbrush of secondary forest (Aeschlimann, 1963) and in primary forest (Brosset, 1969). The density is greatest near the borders of the forest and around clearings. Individuals rarely venture more than 20 to 30 m from cover, and then usually only to eat dripping plants after a rain (Baudenon, 1958). Predators on *C. monticola* include crowned eagles (*Stephanoetus coronatus*), pythons, wild cats, and leopards (Maberly, 1962). Duikers are primarily browsers, feeding on leaves, young shoots, bark, buds, and seeds. They feed to a large extent on the fruit of various trees, which forms an important part of their diet. They graze only to a limited extent (Dorst and Dandelot, 1970). Two stomachs of *C. maxwellii* examined by Aeschlimann (1963) contained the following in abundance: seeds of *Turracanthus africanus* and *Pycnanthus angolensis*; fruits of *Musanga cecropiodes*; and small pieces of mushroom (*Pezize*). Leaves of *Griffonia simplicifolia*, *Ficus barkeri*, *Baphia nitida*, and *Meisteria parvifolia* were also present. It is not known whether this species eats meat, as has been reported for other species of *Cephalophus* (Kurt, 1963). They have been seen to follow noisy bands of monkeys and to eat the fruit knocked down by them. The duikers in turn may be followed by mixed flocks of birds (Brosset, 1969). If fresh green leaves are available, these duikers drink infrequently. If a female is nursing young, however, she may drink 300 gm of water at one time (Aeschlimann, 1963). The following parasites have been reported: blood parasites, *Theileria mutans* (Rousselot, 1949); eight species of ticks (Aeschlimann, 1967); nematodes, *Trichuris ovis* and *Setaria labiata-papillosa*; and cestodes, *Avitellina centripunctata* (Tendeiro, 1948). Although duikers are game animals, they are not sought after by sportsmen because their heads do not make impressive trophies (Walker, 1964). Natives kill them for food, after driving them into nets (Malbrant and Maclatchy, 1949), setting snares on frequently used paths, or attracting them by imitating their alarm whistle (Aeschlimann, 1963). Practical techniques for netting duikers are outlined in Golley and Buechner (1968). "Despite a great deal of hunting pressure (Dorst, 1958; Bourgoin, 1958) it seems clear that this species remains plentiful in most of its range. The large number of exported skins mentioned by these authors is ample indication of its abundance. It can withstand heavy hunting as long as adequate areas of suitable habitat remain available" (Ansell, 1968).

BEHAVIOR. This species has not been studied in the wild but its behavior in captivity has been observed by Rahm (1960), Aeschlimann (1963), and Ralls (1969, 1970, 1971*a*, 1971*b*). Like other duikers it is not gregarious and is usually seen singly or in pairs. It is probably territorial. It is extremely pugnacious in captivity and has been known to chase larger antelopes such as *Cephalophus dorsalis* and *Tragelaphus angasi* (Ralls, 1970). Individuals are especially intolerant of conspecifics of the same sex. An encounter between two males leads almost immediately to a fight, with little of the visual threat display commonly seen in other antelopes (Walther 1958, 1966). They rush at each other and vigorously press together their maxillary glands, first one side of their faces and then on the other side. Both then back up a few steps and rush forward with lowered heads, colliding and pushing against each other head-to-head. After a few such bouts, one turns and runs wildly, often crashing into familiar fences and making spectacular, almost vertical leaps of 2 m or more, while the other pursues him. Adult females also persistently attack any unfamiliar females (Ralls, 1970). Although often said to be nocturnal, *C. maxwellii* frequently is active during the day in the wild (Brossett, 1969) as well as in captivity. Activity is greatest during the early morning, late afternoon, and early evening. When resting, individuals often lie in what Walther (1958) calls the "star formation," with rumps together and heads pointing outward. At night they have been observed lying down, curled up with heads on hind legs, eyes closed, apparently asleep (Ralls, 1971*b*). If pressure is applied to their back, they respond by spreading their hind legs. This reaction, first described by Monard (1938), presumably facilitates travel under low vegetation. One of the most frequent behavior patterns is a rapid up-and-down movement of the tail, which is performed regardless of whether or not insects are present. The function of this wagging is unknown. Rahm (1961) thought it was a sign of "uneasiness" but this seems unlikely as it occurs almost constantly and accompanies most activities. On the contrary, when a duiker is "uneasy" it "freezes," often with one leg off the ground in mid-step, and all motion, including that of the tail, ceases. Two vocalizations are known, an alarm whistle and a loud bleat (Aeschlimann, 1963). The latter is given when picked up by a human or cornered by another duiker. The female squats to urinate; the male stands upright. When a female urinates, a male will often smell and lick the stream of urine, then raise his head and stand rigidly with open mouth and retracted upper lips. This response, termed "flehmen" in German, is found in most ruminants. It is believed that the male is in some way determining the sexual condition of the female (Walther, 1966). Females also sample the urine of males (Ralls, 1971*b*). This behavior has only been reported for a few other species, such as Clark's gazelle (Walther, 1963). The courtship of *C. maxwellii* is less elaborate than that of many other antelopes (Ralls, 1970, 1971*b*). The male "drives" the female and bites at the root of her tail with such force that her hind feet are often lifted off the ground. The tail of an estrous female is usually wet and frayed from the male's chewing and biting. Driving gradually subsides into nose-to-tail circling and mating follows. The male kicks briefly between the backlegs of the female with one stiffly-held foreleg before mounting. This kick, termed "laufschlag" in German, is seen in the courtship of many antelopes, including *C. monticola* (Walther, 1968). Aeschlimann (1963) observed the birth of a calf. It was born head-first after 20 to 30 minutes of labor. The mother ate the fetal membranes and licked the lying calf thoroughly. The vertical tail movements typical of the species were noted as soon as the calf was on its feet. After 25 minutes it fled when frightened. A duiker calf receives a minimum of maternal care. It does not follow its mother but spends most of its time lying alone in a protected spot. It seems to select its own places to hide and searches out its mother to nurse; the female has never been observed to call it out of hiding (Walther, 1968; Ralls, 1970). The typical nursing position is from the side, with the calf's tail directed toward the head of the mother, who licks the anus to stimulate defecation and eats the feces. Growth of the calf is rapid. It first begins to nibble leaves at about 14 days of age (Aeschlimann, 1963). At the same time, the female shows the first signs of weaning behavior and occasionally interferes with attempts to nurse. However, the calf attempts to nurse, often with success, for some weeks. It is completely weaned by 2 months of age. The female grooms the calf frequently by licking its fur. Adults also groom each other in this fashion especially on the head and chest. When kept in groups consisting of one male and two females, the males initiated most bouts of grooming. One of the two females in each group frequently reciprocated but the other did not (Ralls, 1971*b*). Scent marking with the maxillary gland is frequent (Rahm, 1960; Aeschlimann, 1963; Ralls, 1971*a*). When active, males marked environmental objects an average of 5.6 times per 10 minutes. Females that groomed males marked an average of 2.8 times per 10 minutes (type A females), whereas females that did not groom males (type B) marked only .01 times per 10 minutes. Males and type A females tend to increase their marking activity after an additional conspecific of the same sex has been present, but not after one of the opposite sex has been present. Type B females do not. Males and females also rub their glands on each other's glands. They face each other and gently press together the glands first on one side of their faces and then on the other. This behavior may be a ritualized form of the marking seen during fights. It is about 10 times as frequent between the male and type A female of a group as between the male and the type B female. It also occurs between two females, but infrequently. The type A female of a group has a closer relationship with the male, suggesting that the species may normally live in pairs.

GENETICS. The chromosomes of several species of *Cephalophus* have been described by Hard (1969). Although all had the same diploid number ($2N = 60$), *C. maxwellii* had only acrocentric chromosomes, whereas females of other species all had 58 acrocentric chromosomes and two metacentric chromosomes (presumably the X chromosomes).

REMARKS. The Cephalophinae jump into dense cover when alarmed, a habit that led Dutch settlers in South Africa to give them the common name "duiker," which means "diver." *Cephalophus* is from the Greek words *kephale* for "head" and *lophos* for "crest" and refers to the tuft of long hairs on top of the head between and around the horns. The specific name *maxwellii* was given in honor of Colonel Charles Maxwell, who collected the female specimen described by Hamilton Smith.

There is some confusion in the literature as to the boundaries of the genus *Cephalophus*. *Philanthomba* Blyth, 1840 (*Guevei* Gray, 1852, is a synonym) was separated from *Cephalophus* by Pocock (1910) and many later authors because

Philantomba and not *Cephalophus* supposedly lacked inguinal glands. This is untrue, however, for the type species of *Cephalophus* does not have inguinal glands (Ansell, 1969, 1964) and some other species of *Cephalophus* also lack them (Ansell, 1968). For generic synonymy, see Lydekker and Blaine (1914) and Allen (1939). Allen placed *Philantomba* as a synonym of *Cephalophus*, a placement with which I agree.

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