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# *Elaphodus cephalophus* (Artiodactyla: Cervidae)

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***Abstract:*** *Elaphodus cephalophus* Milne-Edwards, 1872 (tufted deer) is usually considered polytypic with 3 or 4 recognized subspecies, depending on the source. It is a small dark chocolate-brown deer typified by a tuft of hair on its crown, sharp upper canines that protrude downward from under the upper lip, and rudimentary antlers on males; it is similar to muntjacs, to which it is closely related. *E. cephalophus* occurs in humid, montane forests at elevations of 300–4,750 m in southwestern through southeastern China and perhaps northwestern Myanmar (historical records). Vulnerable to poaching in remote areas and relatively uncommon in zoos, it is considered vulnerable as a Class II species in China and listed as "Near Threatened" by the International Union for Conservation of Nature and Natural Resources.

***Key words:*** China, mountain forests, Myanmar, near threatened, solitary cervid, Southeast Asia, territorial cervid, tufted deer

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## *Elaphodus* Milne-Edwards, 1872

*Elaphodus* Milne-Edwards in David, 1872:93. Type species *Elaphodus cephalophus* Milne-Edwards, 1872, by monotypy.

*Cervus*: Milne-Edwards, 1874b:unnumbered page opposite of planche 65. Part (*Cervus* [*Elaphodus*] *cephalophus* Milne-Edwards, 1874b).

*Lophotragus* Swinhoe, 1874:453. Type species *Lophotragus michianus* Swinhoe, 1874, by monotypy.

CONTEXT AND CONTENT. Order Artiodactyla, suborder Ruminantia, infraorder Pecora, family Cervidae, subfamily Cervinae, tribe Muntiacini (Groves and Grubb 2011; Mattioli 2011a, 2011b). *Elaphodus* is monotypic. Because of their unique and apparently primitive features, *Elaphodus* and species of muntjacs (*Muntiacus*) have been



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**Fig. 1.**—Mature male *Elaphodus cephalophus* in the Los Angeles Zoo (California), 2 March 2006; note the diagnostic canine teeth and grayish tuft of hair on the top of the head. The pelage is typically described as a dark chocolate-brown, apparent here, but *E. cephalophus* often appears to have more grayish tones on the head and neck, particularly in photographs. Photograph by B. Huffman (www.ultimateungulate.com) used with permission.
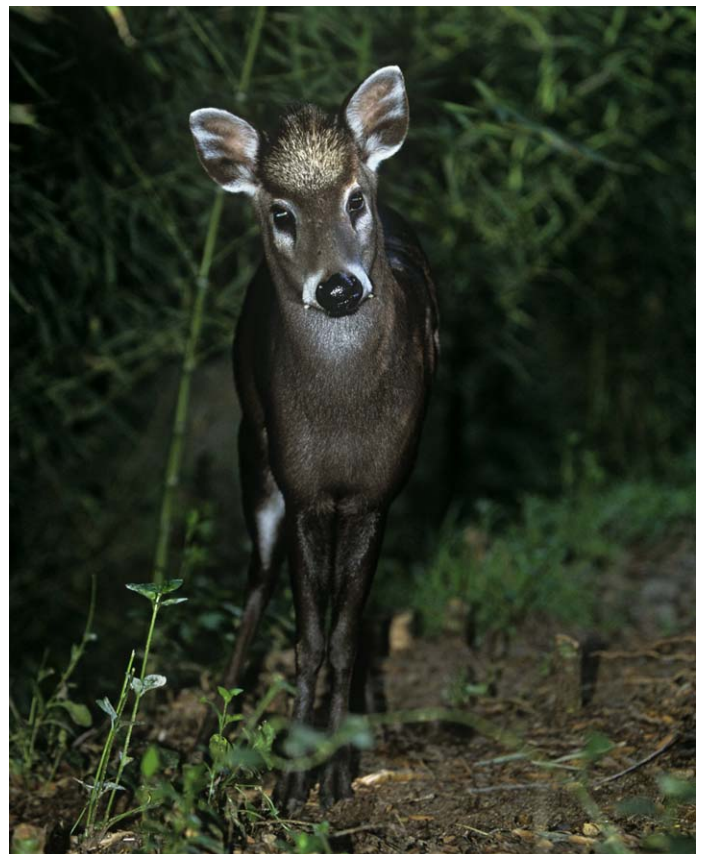
variously grouped in their own family, Muntiacidae (e.g., Bubenik 1990); generically under the subfamily Cervinae (Groves 1974; Grubb 2005); their own subfamily of Cervidae, Muntiacinae (e.g., Putman 1988; Marcot 2007); and their own tribe of the subfamily Cervinae, Muntiacini (e.g., Groves and Grubb 1987, 2011).

## *Elaphodus cephalophus* Milne-Edwards, 1872
### Tufted Deer

*Elaphodus cephalophus* Milne-Edwards in David, 1872:93. Type locality "Moupin" [= Baoxing], Sichuan, western China; first use of current name combination.

*Cervus* (*Elaphodus*) *cephalophus*: Milne-Edwards, 1874b:unnumbered page opposite of planche 65. Name combination.

*Lophotragus michianus* Swinhoe, 1874:453, plate LIX. Type locality "Ningpo" [= Ningbo], Zhejiang Province, eastern China.

*Elaphodus michianus*: Brooke, 1879:900. Name combination.

*Elaphodus ichangensis* Lydekker, 1904:169. Type locality "mountains near Ichang, province of Hupei, Central China."

*Elaphodus michianus fociensis* Lydekker, 1904:169. Type locality "Fing-ling, Fokien, lying considerably to the south of Ningpo;" modified based on the original specimen label to "Kohwang near Ching Feng Ling, about 100 miles northwest of Foochow" by Groves and Grubb (1990:145).

*E*[*laphodus*]. *cephalophus michianus*: Pocock, 1910:956. Name combination.

*Elaphodus cephalophus fociensis*: Lydekker, 1915:38. Name combination.

*Elaphodus cephalophus ichangensis*: Lydekker, 1915:39. Name combination.

*Elaphodus cephalophus megalodon* Hooijer, 1951:11, figure 3. Type locality "Yenchingkou, Wanhsien, Szechwan, China;" fossil from the Pleistocene.

*Elaphodus cepholiphus* Ou, Sheng, and Lu, 1981:111. Incorrect subsequent spelling of *Elaphodus cephalophus* Milne-Edwards, 1872.

*Elaphodus cepholophus* Sheng and Lu, 1982:311. Incorrect subsequent spelling of *Elaphodus cephalophus* Milne-Edwards, 1872.

*E*[*laphodus*] *c*[*ephalophus*] *m ichianus* Wang, Xia, and Hu, 2007:777. Incorrect subsequent spelling of *Lophotragus michianus* Swinhoe, 1874.

*E*[*laphodus*] *c*[*ephalophus*] *m ichianu* Wang, Xia, and Hu, 2007:777. Incorrect subsequent spelling of *Lophotragus michianus* Swinhoe, 1874.

CONTEXT AND CONTENT. Context as for genus. The status of previously named subspecies of *Elaphodus cephalophus* is still somewhat debated. Groves and Grubb (1990) considered the status of *fociensis* and *ichangensis* as provisional because of limited information. In recent assessments, 3 or 4 subspecies have been recognized. Grubb (2005) recognized 4 subspecies: *cephalophus*, *fociensis*, *ichangensis*, and *michianus*, but Mattioli (2011b) recognized 3 subspecies, all of Grubb's except *fociensis*, which was subsumed under *michianus*. Groves and Grubb (2011:86) did not recognize any subspecies, noting that "there is considerable size difference between tufted deer from W China mountains and N Burma [= Myanmar] (skull length 181–202 mm), and those from the coastal mountains of E China (skull length 171–181 mm); but the type of *Elaphodus michianus fociensis* is large, like the W ones." C. P. Groves (pers. comm.) noted, regarding subspecific distinctions, that existing material "was very unsatisfactory and really there was little evidence either way." Much earlier, Allen (1940:1145) when describing *ichangensis* noted that "so few individuals [were available to Lydekker for description] that it is questionable whether it is a valid race with any considerable geographic range, or whether it is best to consider these specimens as intergrades between the typical [*cephalophus*] and the coastal [*michianus*] forms." Allen (1940) considered Lydekker's (1904) *E. m. fociensis*, which was based on a single specimen, to be synonymous with *E. c. michianus*.

Groves and Grubb (2011) were not aware (C. P. Groves, pers. comm.) of the work by Wang et al. (2007), who found separation for 3 subspecies (*cephalophus*, *ichangensis*, and *michianus*) based on differences among 32 cranial characteristics in a recent sample of 32 adult *E. cephalophus* throughout its distribution in China (see "Form and Function"). Their assessment affirmed the following previously recognized subspecies:

*E. c. cephalophus* Milne-Edwards, 1872. See above.
*E. c. ichangensis* Lydekker, 1904. See above.
*E. c. michianus* (Swinhoe, 1874). See above.

Wang et al. (2007) found that 14 and 19 cranial measurements significantly discriminated between *E. c. cephalophus* and *E. c. michianus*, and *E. c. michianus* and *E. c. ichangensis*, respectively. Only 2 cranial measurements differed between *E. c. cephalophus* and *E. c. ichangensis*, suggesting weaker support for the subspecific distinction, as least from the nominotypical form.

NOMENCLATURAL NOTES. The generic name *Elaphodus* is from the Greek words *elaphus* meaning deer and *odous* meaning tooth, referring to the large upper canines in both sexes but more protruding and visible in males. The specific epithet *cephalophus* is from the Greek words *kephale* meaning head and *lophos* referring to the crest or tufts of hair on the top of the head. Toothed deer and head crest aptly describe the tufted deer (Fig. 1).

## DIAGNOSIS

Given its size and distribution, *Elaphodus cephalophus* could be confused with as many as 4 muntjacs (*Muntiacus*), 2 species of musk-deer (*Moschus*), and the Chinese water deer (*Hydropotes inermis*—Wilson and Mittermeier 2011). Relative to dimensions and mass, *E. cephalophus* (head–body length, 100–120 cm; tail length, 7–13 cm; shoulder height, 50–70 cm; mass, 17–30 kg) has a shorter tail and is generally larger in its body dimensions and mass than Reeves's muntjac (*Muntiacus reevesi*, 70–80 cm; 12–13 cm; 45–50 cm; 12–13 kg), the Gongshan muntjac (*M. gongshanensis*, 90–110 cm; 20 cm; 55 cm; 20–25 kg), and the black muntjac (*M. crinifrons*, 90–110 cm; 20 cm; 55 cm; 20–25 kg), but it is comparable to the red muntjac (*M. muntjak*, 90–120 cm; 17–19 cm; 50–70 cm; 20–35 kg—Mattioli 2011a). *E. cephalophus* and the black muntjac share dark pelage coloration (dark brown to grayish with black legs versus black) and have a head tuft (same dark to grayish versus longer haired and golden to yellow); the other muntjacs above are lighter than *E. cephalophus* and range from brown, red-brown, and gray-brown to reddish. The generally smaller, less-known, and allopatric muntjacs are less likely to be confused with *E. cephalophus*: leaf muntjac (*M. putaoensis*), Puhoat muntjac (*M. puhoatensis*), Annamite muntjac (*M. truongsonensis*), and Roosevelt's muntjac (*M. rooseveltorum*—Mattioli 2011a).

Muntjacs and *E. cephalophus* have large upper canines, but those of muntjacs flare somewhat outwardly and are less robust than those of *E. cephalophus* (Allen 1940; Aitchison 1946). Most muntjac species have strongly developed frontal ridges that give rise to elongated antler pedicels, which are short in *E. cephalophus*. The small antlers of male *E. cephalophus* are usually totally obscured by the head tuft (Milne-Edwards 1872; Allen 1940), whereas antlers of male muntjacs arise from elongated furred pedicels, are usually conspicuous, and appear disjunct from the skull proper.

Musk-deer and Chinese water deer have visible upper canines like those of *E. cephalophus* (Aitchison 1946), but musk-deer, in particular, are smaller in body size. Although the black musk-deer (*Moschus fuscus*) is comparable in color to *E. cephalophus*, it is considerably smaller (head–body length, 70–80 cm versus 100–120 cm; tail length, 4–6 cm versus 7–13 cm; mass, 10–15 kg versus 17–30 kg, respectively—Groves 2011; Mattioli 2011b). Unlike *E. cephalophus*, the throat and chest of the forest musk-deer (*M. berezovskii*) are marked with 3 wide, longitudinal stripes (Groves 2011), and like the black musk-deer, it is smaller than *E. cephalophus* (70–80 cm versus 100–120 cm; 3–4 cm versus 7–13 cm; 6–9 kg versus 17–30 kg—Groves 2011; Mattioli 2011b). In contrast to the dark color of *E. cephalophus*, the pelage of the Chinese water deer is reddish brown in summer and becomes paler in winter (Mattioli 2011a).

## GENERAL CHARACTERS

Milne-Edward's (1872:93) 1st description of *Elaphodus cephalophus* briefly provided its salient, outward characteristics: sharp, prominent upper canines, particularly on males; "horn of an inch long hidden by a tufted front" [translated from French]; and very dark chocolate-brown pelage (Fig. 1). Garrod (1876:759) described the pelage as "coarse and slightly quill-like," with the body behind the shoulders having hairs that are white at the root and gradually darkening to a rich brown; hairs become darker, to nearly black, on the legs. Winter pelage is very dark, but summer pelage is "more rufous, with the head pale-ticked" (Schwenn 1988:476). Others have provided useful descriptions of *E. cephalophus* (e.g., Milne-Edwards 1874a, 1874b; Sclater 1876; Lydekker 1904, 1907; Allen 1940; Groves and Grubb 1990; Geist 1998).

Except for antlers and larger canines of males, the sexes of *E. cephalophus* are not strikingly dimorphic in mass and coloration (Fig. 1). Antlers of males are "stumplike, unbranched, irregularly or never shed," and on short pedicels that extend "onto the face in the form of weak ridges which follow a curved course to upper orbital margins . . . and gradually fade out—much less pronounced than most species of muntjacs" (Groves and Grubb 1990:144). A captive male at Tierpark Zoo, Berlin, Germany, shed velvet from his 2.5- to 3.5-cm antlers in late July and early August, and both antlers were shed during the following April–May (Pohle 1989). The tiny antlers are obscured by a frontal tuft of bristly, grayish hairs, projecting upward and collectively forming a disk-shape on the front of the forehead (Sclater 1876; Lydekker 1907).

Both sexes have developed upper canines, protruding visibly downward and daggerlike in males (Fig. 1) and often not visible in females—dental dimorphism (Dong 1993a). The tail of *E. cephalophus* is relatively short, white underneath, and "elaborately fringed and tufted with white fur" (Groves and Grubb 1990:138). Ears are small but broad and round, and they are marked with white internally, on their tips, and around their bases (Lydekker 1907; Groves and Grubb 1990). Inner ear markings (Fig. 1) may serve to automimic posterior horns and enhance threat displays, as in other horned and antlered artiodactyls (Guthrie and Petocz 1970; Leslie and Sharma 2009). White also surrounds the eyes and also is present on the side of the muzzle, on the rear ventrum, inside the rear legs, and above the hoofs (Lydekker 1907; Dolan 1971). Lateral hoofs (dewclaws) are 10–12 mm (Groves and Grubb 1990). Scent glands include preorbital, metatarsal (lacking a hair tuft), and interdigital on hind feet (lacking frontal glands). Two pairs of teats are present (Garrod 1876; Pocock 1910; Muller-Schwarze 1987; Geist 1998). General measurements of *E. cephalophus* were provided under "Diagnosis."

**Fig. 2.**—Distribution of *Elaphodus cephalophus* in a large area of southern China from the eastern reaches of the Tibetan Plateau to the southwestern coastal mountains and northwestern Myanmar; occurrence in Myanmar is based on historical records because no recent observations of *E. cephalophus* have been made there (base map from Brigham Young University's Geography Department, https://geography.byu.edu/pages/resources/outlineMaps.aspx).

## DISTRIBUTION

*Elaphodus cephalophus* is found in southwestern through southeastern China (24–34°N, 98–122°E—Fig. 2; Sheng and Lu 1982; Ohtaishi and Gao 1990:figure 8; Whitehead 1993). Early records reported it in northwestern Myanmar, but extensive recent surveys using camera-traps have failed to find it in the country (Francis 2008; Harris 2008a). Although the cranial measurements by Wang et al. (2007) confirmed the 3 subspecies, their distributions were not definitely demarcated; in general, *cephalophus* is found in the western part of the distribution, *ichangensis* in the central part, and *michianus* in the eastern part (Allen 1940; Fig. 2).

In 1978–1980, just over 100,000 *E. cephalophus* were estimated to have been harvested by hunters throughout its distribution, or about 8.6% of the total cervid harvest in southern China (Sheng and Lu 1982). The greatest numbers of *E. cephalophus* were harvested in Sichuan (about 35,600 individuals), Hunan (about 27,200), and Guangzhan (about 14,500—Sheng and Lu 1982). *E. cephalophus* appeared to be least numerous, based on harvest records, in southern Gansu and Anhui (both about 200 individuals harvested), Guangdong (about 300), and Fujian (about 480) and absent in Guangxi (Sheng and Lu 1982). Since then, Sheng and Ohtaishi (1993) estimated a total population of about

500,000 *E. cephalophus*, and Sheng et al. (1998) estimated 300,000–500,000. Unfortunately, little or no description of survey methodology accompanied these estimates, and no recent, systematic, range-wide surveys have been conducted to clarify extant numbers of *E. cephalophus* (Harris 2008a).

## FOSSIL RECORD

Cervidae is a rich family of Eurasian origin with as many as 26 fossil genera and more than 80 fossil species (Dong 1993b)—likely more now. Cervulines of the Miocene were likely precursors of what are now considered the extant species of Muntiacini (*Elaphodus* and *Muntiacus*), with *Euprox furcatus* the "oldest representative of this new lineage" (Bubenik 1990:62). The late Miocene, about 7–9 million years ago, appears to be the time during which the muntjac forms arose (Bubenik 1990; Lan and Shi 1993, 1994; Gilbert et al. 2006; Groves 2007), leading to a speciose group of similar cervoids, characterized by short antlers and protruding "tusks" (upper canines); the latter were used in intraspecific encounters such as territorial defense and breeding contests (Bubenik 1990). The split between *Elaphodus cephalophus* and muntjacs may have occurred about 3.4–4.8 million years ago (Lan and Shi 1993, 1994; Hernández Fernández and Vrba 2005). Groves and Grubb (1990:165) considered *E. cephalophus* to be "the most primitive surviving muntiacid," with most species of muntjacs more derived, with some extant forms 1–2 million years old (Lan and Shi 1993, 1994).

At present, the earliest fossil form of the Muntiacini lineage is *Muntiacus leilaoensis* from Yuanmou, Yunnan, China; these fossils were dated from the late Miocene 7–9 million years ago (Dong et al. 2004). The 1st fossil remains of ancestors of *Elaphodus* were found in Pleistocene deposits in Yenchingkou, Sichuan, China, from which a larger subspecies, *E. cephalophus megalodon*, was described by Hooijer (1951). This form had larger teeth and broader nasals that were less posteriorly compressed than those of extant *E. cephalophus*, and together these features suggested "the diminution in size which this species has undergone in the course of the Quaternary" (Colbert and Hooijer 1953:115).

## FORM AND FUNCTION

The skull of *Elaphodus cephalophus* is small relative to most other species of extant Cervidae and features prominent upper canine teeth, primitive for cervids, and enlarged preorbital glands in both sexes (Fig. 3)—reminiscent of the primitive four-horned antelope (*Tetracerus quadricornis*—Leslie and Sharma 2009). Based on a recent assessment of cranial measurements from 32 adult specimens of *E. cephalophus*, Wang et al. (2007) concluded that 3 subspecies

**Fig. 3.**—Ventral, dorsal, and lateral views of skull and lateral view of mandible of an adult male *Elaphodus cephalophus* (The Natural History Museum, London, specimen 11.9.8.44); upper canines, particularly large preorbital openings, and reduced and convergent antler pedicels (on males only) are characteristic. Greatest length of skull is 196.0 mm.

were valid: *cephalophus*, *ichangensis*, and *michianus*. Representative subspecific skull measurements (mm ± *SD*) from Wang et al. (2007:table 1) were: greatest length of skull—*cephalophus* 197.80 ± 1.35, *ichangensis* 194.01 ± 2.07, and *michianus* 185.06 ± 1.25; condylobasal length—*cephalophus* 185.34 ± 1.89, *ichangensis* 183.09 ± 1.48, and *michianus* 173.80 ± 1.39; zygomatic breadth—*cephalophus* 82.84 ± 1.35, *ichangensis* 85.44 ± 1.21, and *michianus* 80.12 ± 0.78; and toothrow length—*cephalophus* 62.03 ± 1.06, *ichangensis* 60.86 ± 0.69, and *michianus* 58.06 ± 0.8. The dental formula of *E. cephalophus* is i 0/3, c 1/1, p 3/3, m 3/3, total 34; lower canines

are incisiform and "incorporated into the incisal row," as in species of Artiodactyla (Ungar 2010:158).

Although widely distributed elevationally, *E. cephalophus* can live in high-elevation areas, up to 4,750 m, with associated low temperatures, intense solar radiation (although it tends to stay below tree line and in forest cover), and limited oxygen availability. No particular adaptations of *E. cephalophus* to living in such extremes have been studied, as they have been for other larger mammals in western Asia such as the white-lipped deer (*Przewalskium albirostre*—Leslie 2010), the wild yak (*Bos mutus*—Leslie and Schaller 2009), and the chiru (*Pantholops hodgsonii*—Leslie and Schaller 2008). *E. cephalophus* is generally crepuscular in its daily activity with 2 feeding periods early and late in the day (Liu et al. 2013), but detailed activity budgets have not been established.

Garrod (1876) summarized his detailed examination and necropsy of a male, first described as *Lophotragus michianus*, that died in the living collection of the Zoological Society of London on 14 July 1876. Garrod's conclusion was that the specimen was an eastern form of *Elaphodus*, now considered the subspecies *E. c. michianus*. Anatomically, the specimen shared common characteristics with muntjacs. Its small intestine was 23 feet 2 inches (7.06 m) long, its large intestine was 9 feet 8 inches (2.94 m) long, and its cecum was 9.25 inches (0.23 m) long. Garrod (1876:763) noted that the brain was "richly convoluted for its size." The glans penis was "an elongated cone, terminating much like the tip of a wooden pen-holder, the urethral orifice being situated just behind the extreme tip, slightly turned upwards" (Garrod 1876:764).

Wu et al. (2007) provided a thorough assessment of the blood of 5 young, 2 subadult, and 7 adult *E. cephalophus* in Chengdu Zoo, Sichuan, China, including standard blood profiles and chemistry and biochemical indexes. Ranges of means of representative hematological values were: hematocrit, 56–61%; red blood cells, $12.77–14.17 \times 10^{12}$ cells/ml; hemoglobin, 173.57–184.5 g/l; mean corpuscular volume, 40.48–44.23 $\mu m^3$; and white blood cells, $1.65–3.00 \times 10^9$ cells/ml (Wu et al. 2007). Ranges of mean protein content and biochemical indexes of the blood of the same sample of mix-aged *E. cephalophus* were: total protein, 58.88–66.20 g/l; albumin, 35.12–40.05 g/l; globulin, 23.76–26.15 g/l; and albumin:globulin ratio, 1.5–1.53 (Wu et al. 2007).

Species of *Muntiacus* have "a subterminal light band on hairs, usually over most of the body surface, [but] hairs with this agouti pattern are restricted to the head and neck of *Elaphodus*" (Groves and Grubb 1990:138). Guard hairs of *E. cephalophus* are "curved slightly, with 3–4 waves in the medial portion" (Sheng et al. 1993:74). Characteristics of their guard hairs in winter are: length, 33.4 mm ± 20.3 *SD*; pelage depth, 9.8 mm ± 3.2 *SD*; mean medullary width, 280 μm; mean cortical width, 7.5 μm; and minimum and maximum diameter in cross section, 155–295 μm (Sheng et al. 1993:tables 1 and 2). A relatively high medullar index (width of the medulla

**Fig. 4.**—Weighing a neonatal *Elaphodus cephalophus* at Front Royal (Virginia), Smithsonian Conservation Biology Institute, National Zoological Park; note light tan-brown hoofs of the neonate that blacken with age and characteristic midline spots that fade with age. Photograph by L. Ware used with permission.

divided by the diameter of the hair shaft) of guard hairs from *E. cephalophus* was comparable to that of other Chinese cervids that inhabit cold climates (Sheng et al. 1993).

## ONTOGENY AND REPRODUCTION

Aspects of the reproductive anatomy of *Elaphodus cephalophus* have been described from 2 captive females from the San Diego Zoo, California (Benirschke 2004). The villous placentas from 2 gravid females, one early term and the other late term, had large allantoic sacs, attached to the base of the umbilical cord, and weighed 95 g and 400 g, respectively (Benirschke 2004). The late-term placenta had 5 large and flat cotyledons (maximum diameter = 11 cm), in contrast to the early-term placenta, which had only 2 cotyledons; the nonspiraled 20-cm by 2-cm umbilical cord associated with the late-term placenta had 4 large blood vessels and a large allantoic duct (Benirschke 2004). The general appearance of the fetal–maternal barrier was like that of other deer species (Benirschke 2004).

Age at sexual maturity of female *E. cephalophus* is about 0.8 years (Sheng and Ohtaishi 1993), with the 1st parturition at about 1.5 years (Hayssen et al. 1993). Gestation has been reported from about 180 days (Nowak 1991; Hayssen et al. 1993) to 210 days (Sheng and Ohtaishi 1993; Benirschke 2004; Wu et al. 2005), and a single offspring is the norm (Sheng and Lu 1982; Hayssen et al. 1993). *E. cephalophus* is a seasonal breeder, and mating in late autumn leads to parturition in late spring to early summer (Sheng and Lu 1982; Hayssen et al. 1993; Sheng and Ohtaishi 1993). Only

limited published data on the physical attributes of neonates are available (Sheng and Lu 1982; Pohle 1989). Young are born with spots along their midline that fade with adult pelage (Fig. 4). In a sample of fifteen 0.5- to 6.5-year-old females collected in Sichuan in 1978–1981, 10 females were pregnant, and ranges of fetal mass and fetal body length (variable gestation length) were 18–510 g and 4.0–25 cm, respectively (Sheng and Lu 1982).

## ECOLOGY

***Population characteristics.***—Maximum life span of *Elaphodus cephalophus* in the wild is probably 10–12 years. A captive-born male from Chengdu Zoo, China, transferred 1st to Tierpark Berlin, Germany, and then to the San Diego Zoo (Schwenn 1988; Pohle 1989), lived at least 22 years and 8 months (Weigl 2005). A captive-born female from Tierpark Berlin lived 19 years and 2 months after transfer to San Diego (Weigl 2005). Those are exceptional longevity records; other captive individuals have lived 6–13 years. Eye-lens weight is correlated positively with age, although data beyond 3.5 years are limited for *E. cephalophus* (Sheng 1983). No systematic attempts have been made to estimate densities of *E. cephalophus*; it is no doubt difficult to observe because of its solitary habits, cryptic coloration, and wide distribution and occupation of varied habitats that are typically forested, often with substantial understory (Zhang et al. 2004).

***Space use.***—*Elaphodus cephalophus* inhabits "high, damp forests up to the tree line and close to water" (MacKinnon 2008:462; Fig. 5). It lives in montane areas at elevations as low as 300 m in coastal provinces of southeastern China to as high as 4,500–4,750 m in Sichuan and Gansu provinces on the eastern flank of the Tibetan Plateau (Sheng and Lu 1982; Ohtaishi and Gao 1990:figure 8; MacKinnon 2008:462).

During a 1981 assessment of 3 giant panda (*Ailuropoda melanoleuca*) reserves in the mountains that rim Sichuan, *E. cephalophus* was 1 of the few large mammals observed in 4 of the 5 major mountainous habitat types in the reserves: northwestern mountains, western escarpment, Tibetan, and central basin, but not in subtropical areas (Seidensticker et al. 1984). In a more recent study in the same general area, *E. cephalophus* used low-elevation hillsides with relatively high shrub density and herbaceous plant cover and low bamboo density (Zhang et al. 2004), in contrast to sympatric giant pandas and red pandas (*Ailurus fulgens*) that mainly used upper hillsides and areas of high bamboo density. In spring in Fengtongzhai Nature Reserve in Sichuan Province, China, *E. cephalophus* preferred broad-leafed forests on low-elevation slopes of 20–30° with sunny exposures, access to water, and free of disturbance (Liu and Hu 2008). Broad-leafed forests were also noted as preferred habitat of *E. cephalophus* in Niubeiliang National Nature Reserve,

**Fig. 5.**—Typical forested habitats of *Elaphodus cephalophus* in southern China tend to have open understories but often with abundant shrubs (not obvious here) and herbaceous vegetation for cover and food. Photograph taken during the camera-trap surveys of Li et al. (2012) in Sichuan, Gansu, and Shaanxi provinces, China, and freely available at Smithsonian Wild (www.siwild.si.edu).

Shaanxi (Zeng et al. 2007), and Tangjiahe Reserve, Sichuan, where they were found significantly disjunct from human settlements (Wang et al. 2006).

*Elaphodus cephalophus* is said to patrol its territory along regularly used trails (Geist 1998), making it susceptible to snares (Harris 2008a). Sizes of annual and seasonal territories are unknown, but they are presumably small.

*Diet.*—*Elaphodus cephalophus* is considered to be a generalist ruminant, despite its small size suggesting a more specialized diet high in protein and low in fiber. Methane production from methanogenic bacteria in feces of *E. cephalophus* averages 423 CH$_4$ nmol g$^{-1}$ h$^{-1}$, the highest level for any Cervidae yet studied but still comparable to other ruminal and cecal digesters (Hackstein and van Alen 1996). It eats a variety of "bamboo, forbs, fruit, grass," and browse (Sheng and Lu 1982; Zhang et al. 2004; Mattioli 2011b:409). In captivity, *E. cephalophus* will stand on its hind legs to reach forage (Schwenn 1988).

Winter diets of *E. cephalophus*, based on evaluation of 18 rumen samples from harvested individuals in southeastern China, were dominated by evergreen shrubs: Chinese sweetspire (*Itea chinensis* var. *oblonga*, Iteaceae), Indian hawthorn (*Rhaphiolepsis indica*, Rosaceae), Chinese fringe flower (*Loropetalum chinense*, Hamamelidaceae), Chinaroot or sarsaparilla (*Smilax glabra* and other *Smilax* species, Smilacaceae), and sea bilberry (*Vaccinium bracteatum*, Ericaceae—Ou et al. 1981). Perennial herbs such as *Veronicastrum villosulum* (Plantaginaceae) also were consumed during winter (Ou et al. 1981). Eighteen additional rumen samples collected in winter contained 17 plant species

from 14 families, dominated by species of Liliaceae, Ericaceae, Rosaceae, and Saxifragaceae and with fruits and seeds comprising 10.9% of the diets (Sheng and Lu 1982). *E. cephalophus* also may eat carrion (Huffman 2004), and a captive male ate "garden snails" in his enclosure at the San Diego Zoo (Schwenn 1988:477).

*Diseases and parasites.*—Diseases and parasites of *Elaphodus cephalophus* are unknown in the wild. In the Fort Worth Zoo, Texas, 1 *E. cephalophus* died from malignant catarrhal fever, with the source of disease coming from captive mouflon (*Ovis aries*) and aoudad (*Ammotragus lervia*—Lung et al. 1999). Positive antibodies to bovid gammaherpesvirus, likely associated with ovine herpesvirus 2 and causing malignant catarrhal fever, were found in 1 captive *E. c. michianus* (Mensink et al. 1997). Four of 8 *E. cephalophus* in a "wildlife first-aid centre" in eastern China tested positive for hepatitis-E virus but showed no signs of a recent infection (Zhang et al. 2008a:1021).

*Interspecific interactions.*—Although *Elaphodus cephalophus* can occur with a variety of potentially competitive herbivores (e.g., Zeng et al. 2007; Li et al. 2012; see "Diagnosis" section), no research has been done on potential interspecific interactions. Predators within the range of *E. cephalophus* could include tigers (*Panthera tigris amoyensis*—Mazák 1981), Asiatic leopards (*P. pardus fusca*—Sunquist and Sunquist 2002, 2009), dholes (*Cuon alpinus*—Cohen 1978), and perhaps Asiatic black bears (*Ursus thibetanus*—Li et al. 2012), although populations of these predators have been greatly reduced in recent decades and tigers may be extinct in Hunan, Guangdong, Jiangxi, Fujian, and Zhejiang provinces of southern China (Tilson et al. 2004).

In a 7-year study of diets of Asiatic leopards in Wolong Reserve, Sichuan, China, in 1981–1987, remains of *E. cephalophus* were found in 85.1% of 168 leopard scats in 1981–1983, 29.5% of 104 scats in 1984–1985, and 16.1% of 62 scats in 1985–1987 (Johnson et al. 1993). Although *E. cephalophus* decreased in leopard diets from 1981 to 1987, frequencies of Chinese bamboo rats (*Rhizomys sinensis*) and forest musk-deer increased, which may have been related to an 82% die-off of arrow bamboo (*Bashania fangiana*, Poaceae), making it more difficult for leopards to prey on *E. cephalophus* without detection (Johnson et al. 1993).

## HUSBANDRY

*Elaphodus cephalophus* is relatively uncommon in zoos in Europe and the United States, with the 1st specimens leaving China in the mid-1980s (Dolan 1986; Schwenn 1988; Pohle 1989). According to the International Species Information System (www.isis.org, accessed 3 February 2013 by B. Huffman, pers. comm.), a global database for animals in zoos and aquariums, 87 *E. cephalophus* (47 males,

39 females, and 1 unsexed neonate) were held in 6 European and 18 United States zoos through 2012. In the United States, the largest holdings are at the Smithsonian Conservation Biology Institute at Front Royal, Virginia (6 males and 8 females); San Diego Zoo, California (6 males and 3 females); and Bronx Zoo, New York (4 males and 5 females). Zoos in the United States hold *E. c. cephalophus*, whereas *E. c. michianus* is held in Europe (B. Huffman, pers. comm.). The 1st *E. c. cephalophus* in the Western Hemisphere arrived at the San Diego Zoo in late 1985 (Dolan 1986; Schwenn 1988).

*Elaphodus cephalophus* can be challenging to breed in captivity; only 6 captive births occurred in 2012 (B. Huffman, pers. comm.). At Chengdu Zoo in Sichuan, China, special diets and secluded habitats with native plants were provided to enhance breeding, which resulted in 4 births by 3 females in the 2 years following improvements to the captive conditions (Wu et al. 2005). Females were fed mixed diets of 0.2 kg of apples, 0.25 kg of corn, and 0.07 kg of native vegetation, containing ≥ 17% crude protein, ≤ 10% fiber, 1–1.5% calcium, ≥ 0.5% phosphorus, 2.5% fat, and 11,009.2 kJ/kg digestible energy (Wu et al. 2005). Energy contributions in the daily diet were 51.7% from corn, 23.8% from apples, and 24.5% from native vegetation.

At Twycross Zoo of the East Midland Zoological Society, Warwickshire, United Kingdom, 2 male *E. cephalophus* were housed separately because of territorial fighting but had access to a large grassy area on a rotational basis (Rose at al. 2007). They were fed "predominantly chopped vegetables and fruit mixed with concentrates and oats" but also given branches and leaves of willow (*Salix alba*), beech (*Fagus sylvatica*), cherry (*Prunus*), horse-chestnut (*Aesculus hippocastanum*), ash (*Fraxinus excelsior*), and basswood (*Tilia*—Rose et al. 2007:7). Novel foods such as mushrooms, sweet corn, apricots, blueberries, and grapes were provided sparingly "to recreate a mix of plant-like materials that are [presumably] consumed in the wild" (Rose et al. 2007:9). Structure provided by the branches of supplemental foods and other "furnishings" in the pens enhanced opportunities for the male *E. cephalophus* to scent mark their "territories," an important part of their behavioral repertoire and activity budget in the wild (Rose et al. 2007).

The 1st *E. cephalophus* to be exhibited in the United States arrived at the San Diego Zoo, California, on 31 December 1985 (initially 2 males, followed by a female in 1986—Dolan 1986; Schwenn 1988). The 2 males undertook a complicated multistep itinerary of travel and quarantine; they originated in Sichuan, China, passed through Berlin's Tierpark Zoo for a 6-month quarantine (Pohle 1989) and then additional quarantine in Hamburg, Germany, and New York City before final shipment to San Diego. They were fed alfalfa ad libitum, occasional *Acacia* browse, and a mixture of "herbivore pellets, horse sweet feed (14% protein), omnivore biscuits, carrots, yams, apples, kale,

and Romaine lettuce" (Schwenn 1988:477). Conditions were suitable enough for the female to give birth to a healthy offspring in June 1987, followed by a stillbirth in March 1988 likely caused by "fetal hypoxia … [from] premature placental separation" (Schwenn 1988:480). As with the specimens at Twycross Zoo, those in San Diego spent considerable time scent marking, notably with the large preorbital gland and mouth, and although frontal glands on the forehead are not known for *E. cephalophus*, the males rubbed their foreheads "in a continuous up and down motion … on bark and vegetation" (Schwenn 1988:480). Both sexes also scraped the ground with their front feet in combination with extensive marking with their preorbital glands, urination, and defecation.

## BEHAVIOR

Very little is known about the behavior of *Elaphodus cephalophus* in the wild. Aside from the mating period and when females raise young, both males and females are presumed to be solitary and territorial (e.g., Geist 1998; Huffman 2004), maintaining their territories with frequent scent marking—based mostly on observations of captive individuals (e.g., Schwenn 1988; Rose et al. 2007). At the San Diego Zoo, dung piles or latrines were used repeatedly and likely represented a way to communicate presence, ownership, and condition, as is seen in other species of small Cervidae (Schwenn 1988) and many species of Bovidae (Groves and Leslie 2011).

The following descriptions of behaviors were provided by Schwenn (1988) from her observations of captive *E. cephalophus*. Self-grooming was common, whereas allo-grooming was largely limited to female–female dyads; they were described as "fastidious groomers." Their preorbital glands were frequently cleaned with their long tongues, particularly after scent marking. Alarm usually resulted in freezing rather than fleeing. Vocalizations included "barking" (heard during alarm and courtship), high-pitched "whining" (heard under stress by a subordinate individual during confrontations with a dominant), and closed-mouth "clicking" (heard during regular interactions, exposure to a new area, and seemingly during courtship—perhaps unique to *E. cephalophus*). The latter 2 vocalizations were often accompanied with "sneers" and "sneer/whine" facial expressions, exposing upper canines. Male–male interactions resulted in dominant and submissive behaviors, with the dominant male chasing and head butting the subordinate male and the latter responding with sneers and sneer/whines and adopting submissive postures such as crouching, crawling, and lying down. The daggerlike canines of mature males (Fig. 6) no doubt play a role in such interactions and in territorial defense in the wild. Hairs on the tail, forehead, and entire body were flared at these times. *E. cephalophus* is
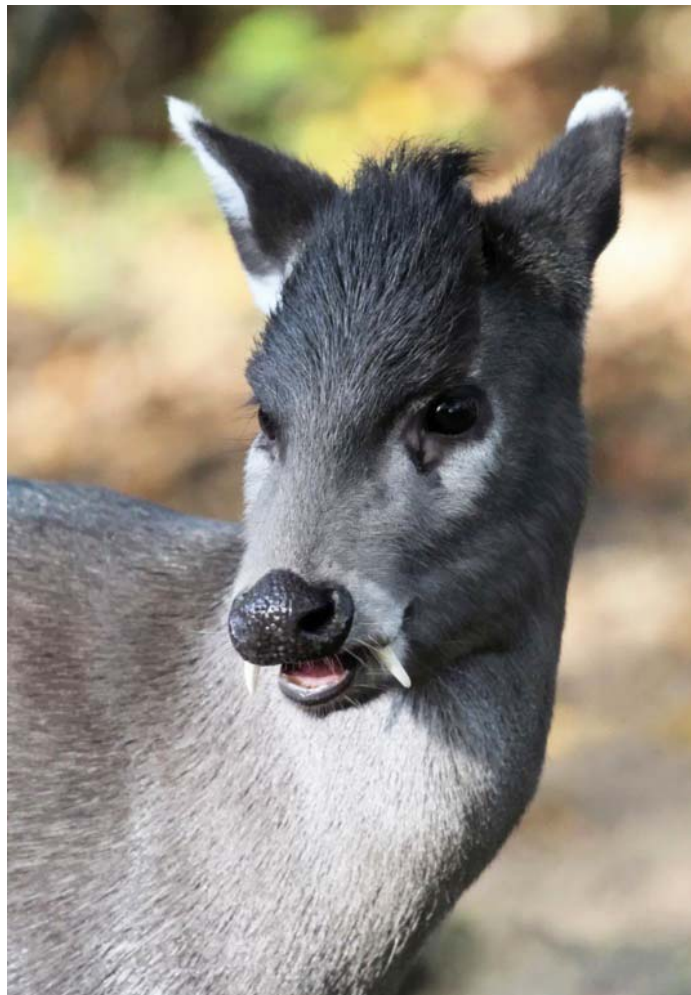
**Fig. 6.**—Developed upper canine teeth, tufts on hair on the top of the head, and white-tipped ears are characteristic of male (pictured here) and female *Elaphodus cephalophus*; only males have antlers, but they are typically obscured by the crown tuft and perhaps rarely shed (unlike annually shedding of antlers by other species of Cervidae). Photograph taken at the Zoologischer Garten Magdeburg, Germany, by Николай Усик (http://paradoxusik. livejournal.com), available under the Creative Commons Attribution–Share Alike (http://en.wikipedia.org/wiki).

agile and flees with "catlike jumps," with its tail upright and wagging, exposing the white underside (Geist 1998:47)

## GENETICS

Chromosomal diploid numbers (2n) of *Elaphodus cephalophus* are 46–48 for females and 47–48 for males, and the fundamental number (FN) is 52 (Shi 1981; Wang and Quan 1984; Fontana and Rubini 1990; Shi et al. 1991; Kong et al. 2001, 2002; Nian et al. 2006). Males have a pair of large heteromorphic chromosomes, "rich in constitutive heterochromatin," as shown by C-banding (Cao et al. 2005:512). Sex chromosomes of *E. cephalophus* are polymorphic: the large telocentric X-chromosome is without secondary constriction and the Y-chromosome is a medium-sized subtelocentric (Cao et al. 2005; Huang et al. 2006; Zhang et al. 2008b). At least 3 Robertsonian translocations and "9 tandem chromosomal fissions involving 14 ancestral chromosomal arms" have occurred during the evolution of *E. cephalophus* (Huang et al. 2006:29).

As in other mammals, the mitochondrial genome of *E. cephalophus* is about 16,000 base pairs (bp) long, with 22 transfer RNA genes, 13 protein-coding genes, and 2 ribosomal RNA genes, and phylogenetic analyses support a sister relationship with muntjacs (Pang et al. 2008). The entire genome size of *E. cephalophus* has been estimated at $2.43 \times 10^9$ bp (Wang et al. 2008). The exon 2 region of the p16[INK4] gene of *E. cephalophus* has been successfully cloned (Cao et al. 2001). A cDNA library from cerebrum tissue of *E. cephalophus* has been synthesized, containing $5.1 \times 10^5$ plaque-forming units/ml of cloned material (Tang et al. 2006). Forensically, genetic fingerprinting using an oligonucleotide probe has been used to differentiate among protected Chinese cervids, including *E. cephalophus* (Fang and Wan 2002; Wan and Fang 2003; Wan et al. 2003).

## CONSERVATION

*Elaphodus cephalophus* is protected as a Class II species in China (Harris 2008a, 2008b) and is currently classified as "Near Threatened" by the International Union for Conservation of Nature and Natural Resources, although overhunting and projected population decline of less than but perhaps near 30% in the next 3 generations (about 10 years) may necessitate listing it as "Vulnerable" in the near future (Harris 2008a). *E. cephalophus* is not protected under the Appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2012).

Published literature provides a somewhat mixed message on the conservation status of *E. cephalophus*. Sheng and Lu (1982) reported that about 100,000 *E. cephalophus* were harvested annually in the late 1970s and early 1980s in China, with 76% of them coming from Sichuan, Hunan, and Guizhon provinces. That, added to illegal harvest, was probably unsustainable—a situation experienced by many wildlife species in southern China (Harris 2008b). The rapid increase in human population density from west to east across southern China suggests that numbers of *E. cephalophus* are probably far lower than once occurred in its eastern distribution (C. Zou, pers. comm.). Although not quantified, habitat loss from forest harvest and other human activities no doubt negatively affects *E. cephalophus* throughout its distribution. Clearly, more basic research could clarify the conservation status of *E. cephalophus*.

## ACKNOWLEDGMENTS

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