

THE ARTIODACTYLS

Order Artiodactyla

ORDER ARTIODACTYLA

The ordinal name, Artiodactyla, literally meaning “even-digitated ones,” points out the major feature uniting the families of artiodactyls, the even-toed ungulates, and distinguishing these ungulates from the perissodactyls, the odd-toed ungulates. There are usually either two or four digits, and the limbs are **paraxonic**, with the plane of symmetry passing between the third and fourth digits of each foot, which are about equal in size and which equally share the weight placed on that foot (Fig. 27.1). The second and fifth digits, when present, are smaller than the third and fourth, and in many artiodactyls do not touch the ground unless it forms a very soft substrate.

Most living artiodactyls are herbivorous, but some of the more generalized forms (e.g., the hogs) are omnivorous. The types of plant material eaten by artiodactyls range from lichens on the Arctic tundra to fruits and tubers in tropical forests. Wild artiodactyls are important as sources of meat and hides in many cultures and as game animals in others. By far, the largest number of domesticated animal species comes from this order. Domesticated artiodactyls provide meat, hides, and milk and serve as beasts of burden in nearly all parts of the world. These domestic species include the hog, *Sus scrofa*; llama, *Lama glama*; alpaca, *Lama pacos*; Bactrian (two-humped) camel, *Camelus bactrianus*; dromedary (one-humped camel), *Camelus dromedarius*; reindeer, *Rangifer tarandus*; water buffalo, *Bubalus bubalis*; “cattle,” *Bos taurus*; gayal, *Bos frontalis*; domesticated banteng or “Bali cattle,” *Bos javanicus*; yak, *Bos grunniens*; goat, *Capra hircus*; and sheep, *Ovis aries*.

DISTINGUISHING CHARACTERS

The third and fourth digits of each foot are subequal in size, with the main axis of weight passing between them. The second and fifth digits are reduced in size or are absent (Fig. 27.2). The first digit is absent. The metapodials (metacarpals or metatarsals) of the third and fourth digits are the largest and may (Tylopoda, Ruminantia) or may not (Suiformes) be fused to form a “cannon bone.” All digits terminate in hoofs (modified in Camelidae and Hippopotamidae). A unique characteristic of the order is an astragalus with a pulley-shaped articulating surface both proximally and distally.

Cheek teeth range from bunodont (Suiformes) to selenodont (Tylopoda and Ruminantia) and from brachyodont to hypsodont. The full “late primitive” placental dental formula is present in some forms (most Suidae). The upper incisors are lost (Ruminantia) or reduced in number (Tylopoda) in most species. Upper canines are frequently lost (most Ruminantia) or reduced in size (Tylopoda, some Ruminantia). A complete postorbital bar may (Hippopotamidae, Tylopoda, Ruminantia) or may not (Suidae and Tayassuidae) be present.

In many Ruminantia, an antorbital pit (in which the antorbital gland is located) is conspicuous as a depression on the side of the rostrum just anterior to the orbit (Fig. 27.3). A hole or fenestra is present on the rostrum of many ruminants at the point where the frontal, nasal, lacrimal, and maxillary bones meet (Fig. 27.3). Most male Ruminantia have horns or antlers and so do females of some species. The structure of these is different in

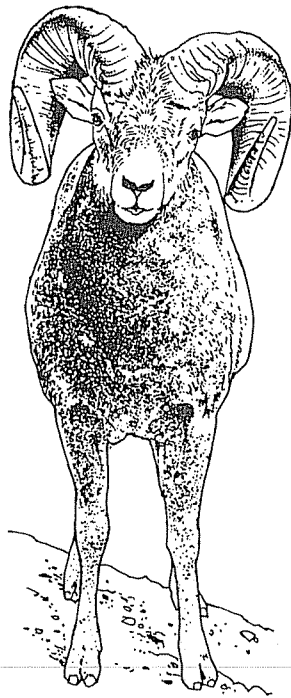


Figure 27.1 A bighorn sheep, *Ovis canadensis*, Bovidae. (Giuliani 1993)

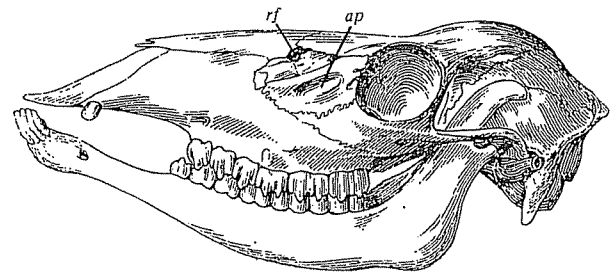


Figure 27.3 Skull of a deer of the genus *Cervus*, Cervidae: ap, antorbital pit; rf, rostral fenestra. (Sokolov 1959)

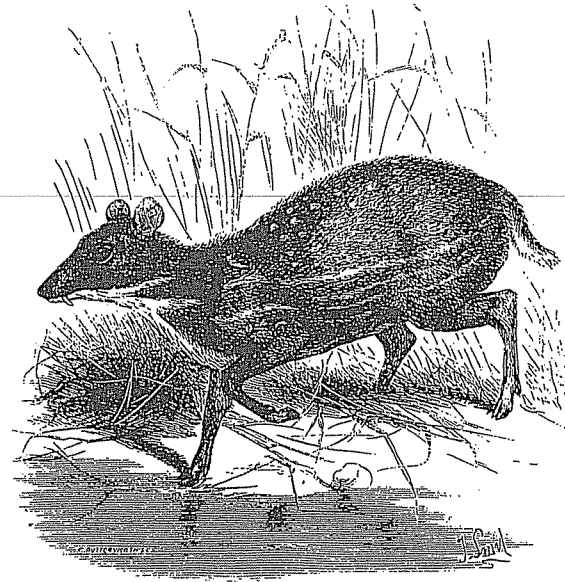


Figure 27.4 The African water chevrotain, *Hyemoschus aquaticus*, Tragulidae. (Flower and Lydekker 1891)

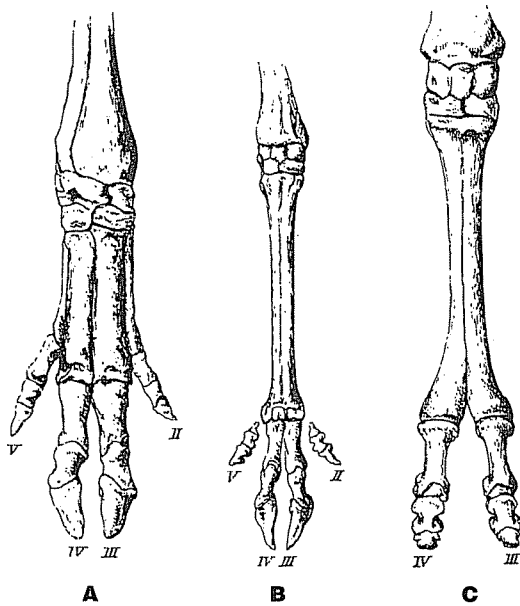


Figure 27.2 Bones of the right forelegs of three representative artiodactyls: (A) a hog, *Sus scrofa*, Suidae; (B) red deer, *Cervus elaphus*, Cervidae; (C) Bactrian camel, *Camelus bactrianus*, Camelidae. Note that in the Suiformes (A), each metacarpal is distinct; in the Tylopoda (C), the metacarpals of digits III and IV are fused for most of their length but separated at their distal end; and in the Ruminantia (B), the two metacarpals are fused for their entire length. Fused metacarpals or metatarsals form what is termed a cannon bone. (Flower and Lydekker 1891)

each of the families Cervidae, Giraffidae, Antilocapridae, and Bovidae. See Chapter 5 for the anatomy and development of these structures. Males of the Tragulidae (Fig. 27.4), Moschidae (Fig. 27.16), and the only cervid, *Hydropotes inermis*, which lacks antlers, are equipped with very long upper canines. Two genera of Cervidae, *Muntiacus* and *Elaphodus*, possess both antlers and long upper canines.

The stomach of nonruminant artiodactyls is a relatively simple, two-chambered structure in Suidae, and a three-chambered structure in Tayassuidae and Hippopotamidae. Among those artiodactyls that ruminate, the stomach is a three-chambered structure in Camelidae and Tragulidae,¹ and is a complex, four-chambered structure

¹In Tragulidae, the stomach is four-chambered, but the omasum is rudimentary.

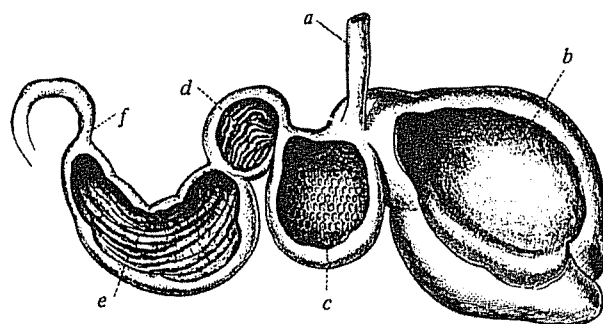


Figure 27.5 A generalized four-chambered “stomach” of a ruminant. a, unmodified portion of esophagus; b, first chamber or rumen; c, second chamber or reticulum; d, third chamber or omasum; e, fourth chamber or abomasum; f, duodenum. (Flower and Lydekker 1891)

(Fig. 27.5) for the breakdown of cellulose by microorganisms, in the remaining five families. The caecum is absent, and the uterus is bicornuate. Testes are scrotal in some species, and a baculum is never present.

LIVING FAMILIES OF ARTIODACTYLA

A list of living families of Artiodactyla, and their contents, is given in Table 27.1.

Artiodactyls are native to all parts of the world’s land surface except Antarctica, oceanic islands, and the great majority of the Australian Region. One species of suid occurs in Sulawesi (= Celebes), Indonesia, and on

nearby islands, thus barely penetrating the Australian Region. Domestic herds and feral populations of domesticated artiodactyls now occur over much of the Australian Region and on many oceanic islands.

KEY TO LIVING FAMILIES OF ARTIODACTYLA

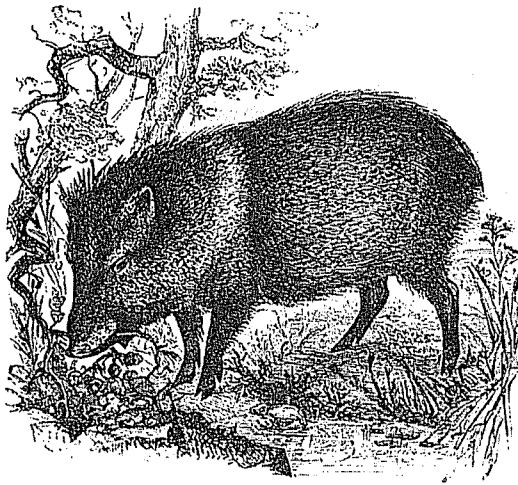
- 1 Postorbital bar absent or incomplete; upper incisors present 2
- 1' Postorbital bar complete²; upper incisors present or absent 3
- 2 (1') Dental formula $2/3 \ 1/1 \ 3/3 \ 3/3 = 38$; upper canines relatively straight, point down (Fig. 27.6B); two or three pedal digits **Tayassuidae**
peccaries
- 2' Dental formula $3/3 \ 1/1 \ 4/4 \ 3/3 = 44$, $1/3 \ 1/1 \ 3/2 \ 3/3 = 34$, or $2/3 \ 1/1 \ 2/2 \ 3/3 = 34$; upper canines curve either outward, upward, or both (Figs. 27.7 and 27.8); four pedal digits **Suidae**
swine, hogs, pigs

²Incomplete in some specimens of hippos.

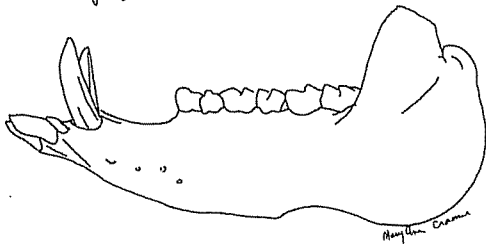
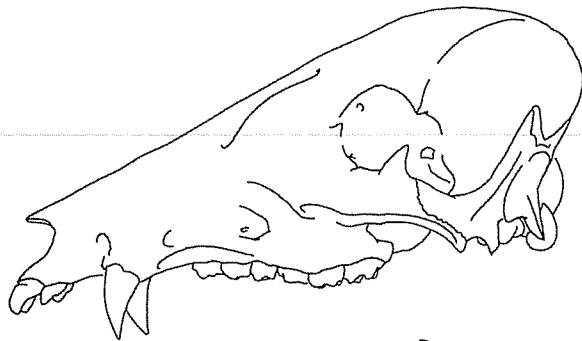
TABLE 27.1 Living Families of Artiodactyla*

Family	Common Name	Number of		Distribution
		Genera	Species	
<i>Suborder Suiformes</i>				
Suidae	Hogs, pigs, or swine	5	16	Ethiopian, Palearctic, Oriental, Sulawesi in Australian
Tayassuidae	Peccaries	3	3	Neotropical, southern Nearctic
Hippopotamidae	Hippos	2	2	Ethiopian
<i>Suborder Tylopoda</i>				
Camelidae	Camels, guanacos, and allies	3	6	Western and southern South America, eastern Palearctic
<i>Suborder Ruminantia</i>				
Tragulidae	Chevrotains	3	4	Portions of Ethiopian and Oriental
Moschidae	Musk deer	1	4	Eastern Palearctic, northern edge of Oriental
Cervidae	Deer	16	42	Holarctic, Neotropical, Oriental
Giraffidae	Giraffe and okapi	2	2	Ethiopian
Antilocapridae	Pronghorn	1	1	Southwest Nearctic
Bovidae	Cattle, antelopes, sheep, goats, and allies	45	137	Holarctic, Ethiopian, Oriental

*Based upon Grubb (1993).



A



B

Figure 27.6 The collared peccary (A), *Pecari tajacu*, Tayassuidae, and a skull (B) from the same species. (A, Flower and Lydekker 1891; B, Mary Ann Cramer)

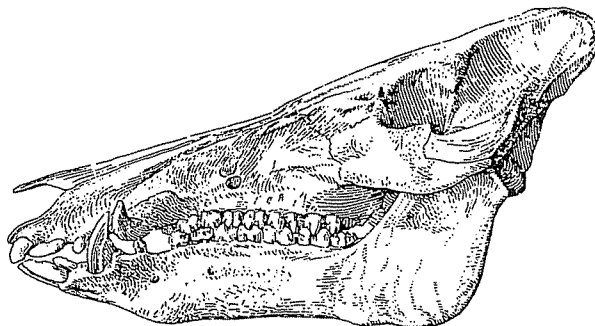


Figure 27.7 The skull of a wild boar, *Sus scrofa*, Suidae. The domestic hog belongs to the same species, but its skull has a more concave dorsal profile. (Gromov et al. 1963)

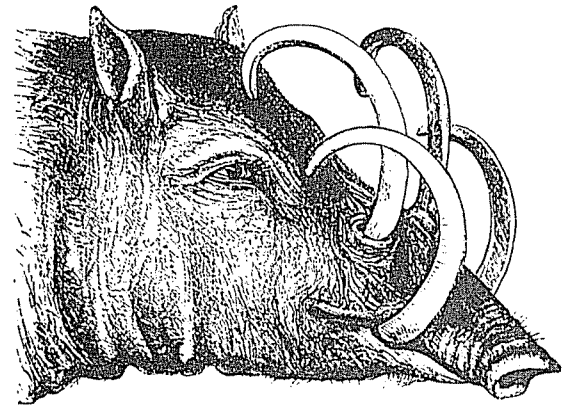


Figure 27.8 The babirusa, *Babyrousa babyrussa*, (yes, each of the three names is spelled differently!) a unique hog (Suidae) confined to Sulawesi (= Celebes) and a few smaller islands of Indonesia. The sockets of the upper canines turn up alongside the rostrum so that the teeth grow dorsally through the skin. The upper and lower canines do not come in contact. (Flower and Lydekker 1891)

- 3 (1') Lower canine alveoli anterior to alveoli of lower incisors (Fig. 27.9B); lower canines larger than upper canines; skull very massive (Fig. 27.9B); rostrum broader distally than proximally **Hippopotamidae**
hippos
- 3' Lower canine alveoli posterior to alveoli of lower incisors (Fig. 27.10); lower canines, if present, smaller or equal in size to upper canines; skull not particularly massive; rostrum narrower distally than proximally 4
- 4 (1') Upper incisors present (Fig. 27.10); hoofs nail-like, with large pads on bottoms of feet posterior to hoofs **Camelidae**
camels, guanacos, and allies
- 4' Upper incisors absent; well-developed hoofs present, pads absent, only hoofs touch ground 5
- 5 (4') Horn cores or antler pedicels present 6
- 5' No indication of horn cores or antler pedicels 9
- 6 (5) Paired "horns" are distinct bones situated over sutures of frontal and parietal bones (Fig. 27.11); a third "horn" sometimes present on midline of skull (Fig. 27.11) **Giraffidae**
giraffe and okapi
- 6' Paired horns or antlers are projections of frontal bone; third medial "horn" never present 7

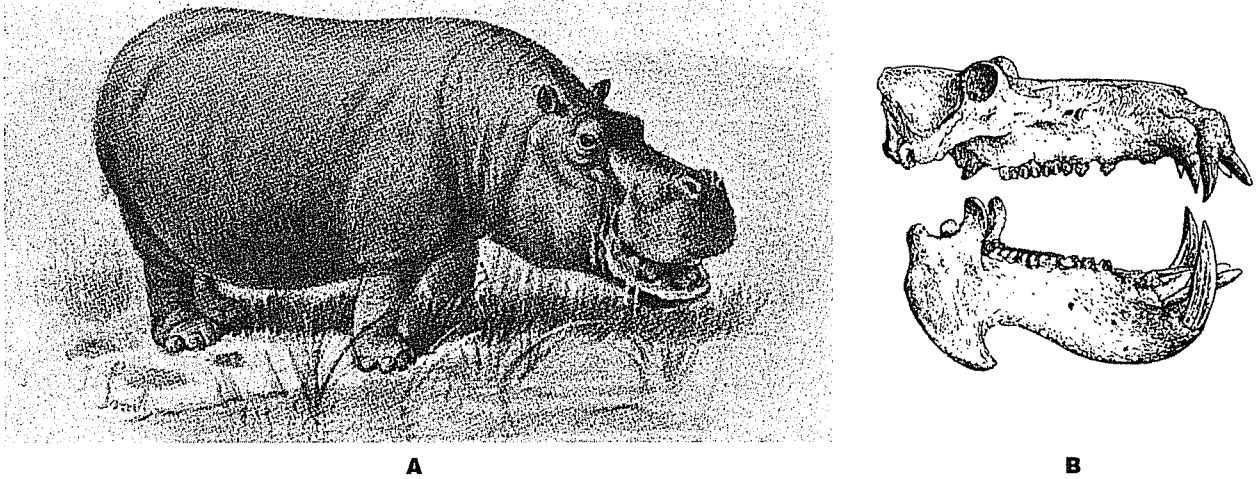


Figure 27.9 A hippopotamus (A) *Hippopotamus amphibius*, Hippopotamidae, and a skull (B) of the same species. (A, Sclater and Sclater 1899; B, Sclater 1900)

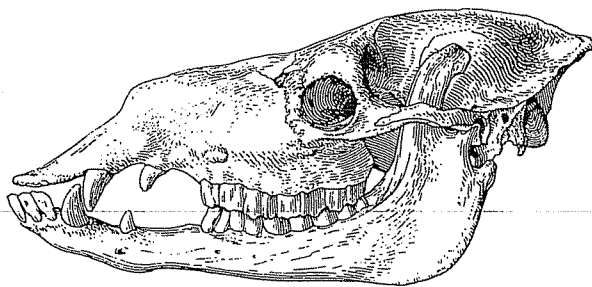


Figure 27.10 The skull of a Bactrian camel, *Camelus bactrianus*, Camelidae. (Sokolov 1959)

- 7 (6') Antlers or antler pedicels present (Fig. 27.12A, B); antorbital pit and rostral fenestra both present (Fig. 27.3) **Cervidae** (in part)
deer with antlers
- 7' Horns or horn cores present (Figs. 27.13, 27.14, 27.15); presence of antorbital pit and rostral fenestra varies, one or both frequently absent ..
..... **8**
- 8 (7') Horn core with sharp anterior edge; one or two large foramina present in frontal at anteromedial base of horn cores (Fig. 27.14A); horn forked, having small anterior projection (Fig. 27.13); digits 2/2 **Antilocapridae** (in part)
most pronghorns, *Antilocapra americana*
- 8' Horn core with rounded anterior edge, or if anterior edge sharp, no foramina in frontal at base of horn core; horn not forked (Fig. 27.15); digits 2/2 or 4/4 **Bovidae** (in part)
horned bovids

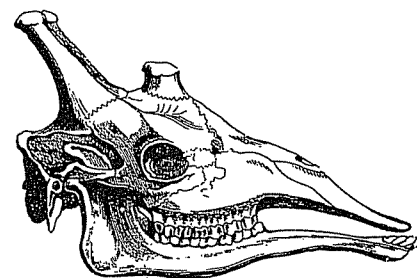
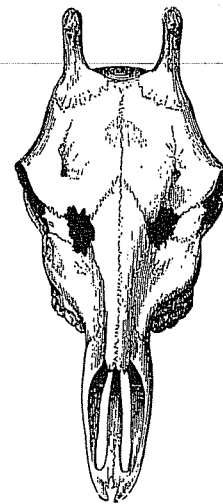
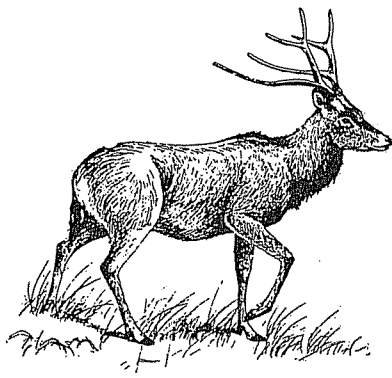
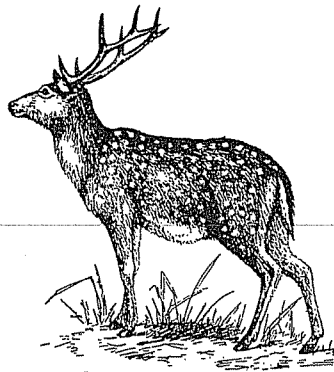


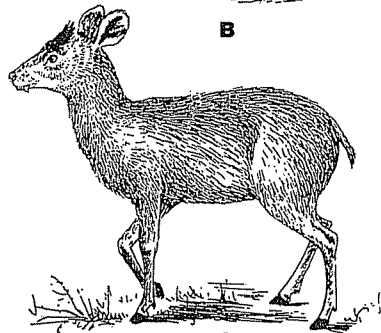
Figure 27.11 Skulls of giraffes, *Giraffa camelopardalis*, Giraffidae. Note that the “horns” (ossicones) are distinct bones and are separated from the frontals by sutures in the specimens figured. They can also completely fuse with the rest of the skull, eliminating obvious sutures. (Dorsal view, Owen 1866; lateral view, Giebel 1859)



A



B



C

Figure 27.12 Representative cervids, Cervidae. (A) Père David's deer, *Elaphurus davidianus*; (B) Sika deer, *Cervus nippon*; and (C) tufted deer, *Elaphodus cephalophus*. Not to same scale.

(Hsia et al. 1964)

- 9 (5') Either antorbital pit absent or rostral fenestra absent or both absent; upper canine teeth absent (Fig. 27.16) 10
- 9' Both antorbital pit and rostral fenestra present, or if one absent, upper canine teeth present (Figs. 27.17 and 27.18) 12
- 10 (9) Antorbital pit absent; rostral fenestra narrow dorsoventrally and elongate anteroposteriorly (Fig. 27.14B) **Antilocapridae** (in part)
hornless female pronghorns, *Antilocapra americana*

- 10' Antorbital pit present or absent; rostral fenestra, if present, not as above 11
- 11 (10') Antorbital pit absent; rostral fenestra very small, less than 4 mm in length; greatest length of skull 100 mm or less **Tragulidae** (in part)
some female chevrotains
- 11' Antorbital pit present or absent, if absent; greatest length of skull more than 100 mm; rostral fenestra usually more than 4 mm in length
..... **Bovidae** (in part)
most hornless female bovids

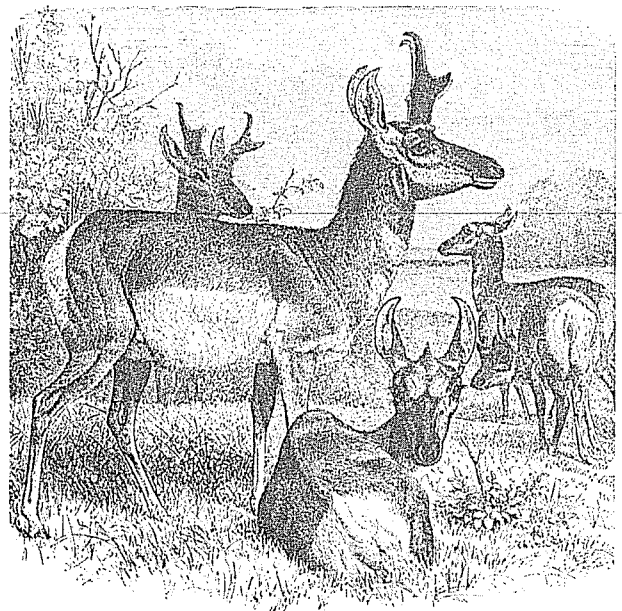


Figure 27.13 Pronghorns, *Antilocapra americana*, Antilocapridae.

(Kingsley 1884)

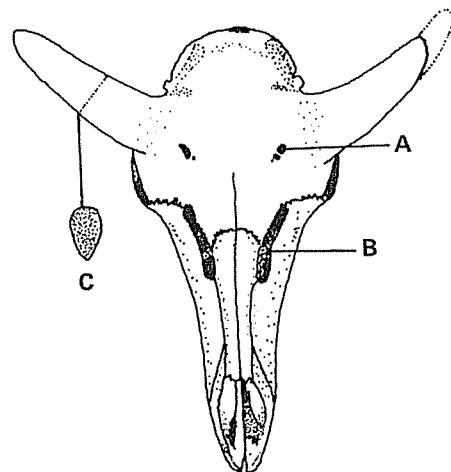
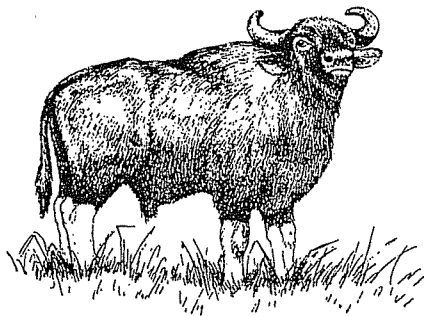


Figure 27.14 The skull of a pronghorn, *Antilocapra americana*, Antilocapridae. (A) Foramen at base of horn core; (B) rostral fenestra; (C) a cross section of horn core.

(G. A. Moore)



A



B



C



D

Figure 27.15 Representative bovids, Bovidae. (A) The gaur, *Bos frontalis*; (B) the takin, *Budorcas taxicolor*; (C) an ibex, *Capra ibex*; (D) a wild sheep, the argali, *Ovis ammon*. Not to same scale. (Hsia et al. 1964)

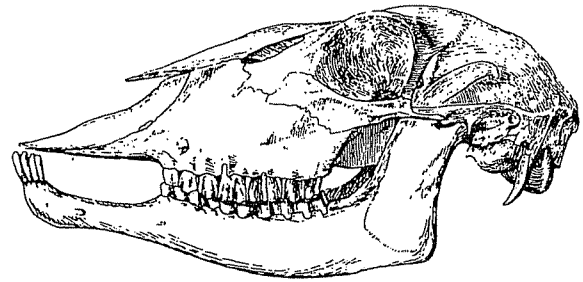
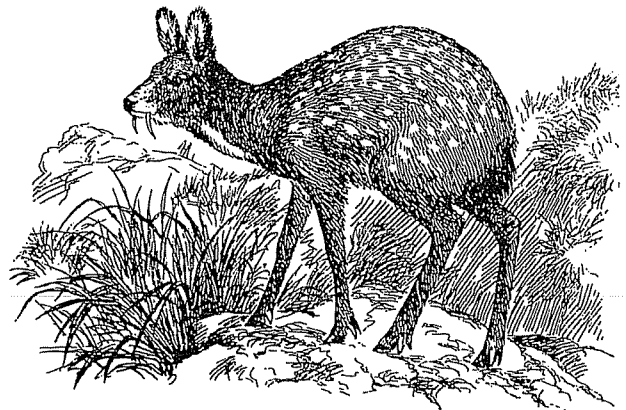
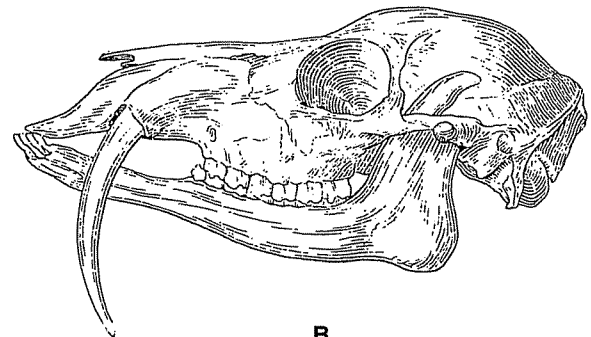


Figure 27.16 Skull of a female gazelle, *Gazella*, Bovidae. (Sokolov 1959)



A



B

Figure 27.17 A musk deer (A) *Moschus moschiferus*, Moschidae, and its skull (B). (Gromov et al. 1963)

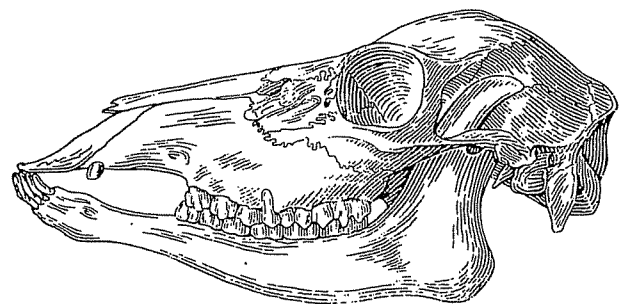


Figure 27.18 Skull of a female sika deer, *Cervus nippon*, Cervidae. (Gromov et al. 1963)

- 12 (9') Antorbital pit absent; upper canines present; condylobasal length less than 100 mm **Tragulidae** (in part)
most chevrotains
- 12' Antorbital pit present; upper canines present or absent; condylobasal length usually greater than 100 mm **13**
- 13 (12) Orifice of lacrimal canal usually single (Fig. 27.19A); upper canines absent **Bovidae** (in part)
some female antelopes
- 13' Orifice of lacrimal canal double (Fig. 27.19B); upper canines present or absent **14**
- 14 (13) Upper canines present in both sexes, relatively long and pointed (Fig. 27.17); glandular slit (preorbital gland) in front of eye absent; size small, head and body length 700–1000 mm **Moschidae**
musk deer, *Moschus*
- 14' Upper canines present or absent; if present and fang- or tusklike, then preorbital gland present; size usually large, head and body length usually more than 1,000 mm **Cervidae** (in part)
deer without antlers (includes females of most species)

COMMENTS AND SUGGESTIONS ON IDENTIFICATION

The structure of the limbs readily distinguishes artiodactyls from members of all other orders. Cranially, the skulls of only perissodactyls could be confused with those of artiodactyls. The large, massive skull and enormous lower canines will serve to identify hippos. Suid skulls may be distinguished from those of tayassuids by the curvature of the upper canines of the former. The rudimentary upper incisors of camelids distinguish them from artiodactyls of other families, and the unique “horns” of the giraffe and okapi identify that family.

Cervids, antilocaprids, and bovids having antlers or horns are easily identified by those structures. However, the “hornless” ruminants are more difficult to distinguish. Their lack of upper incisors identifies them as artiodactyls, but their identification to family is more difficult. Tragulids (and moschids) have large upper canines; however, there are some species of small cervids that also have long upper canines. The Tragulidae have a tiny rostral fenestra and no antorbital pit. The long-canined, antlerless cervids also have a small rostral fenestra but do have an antorbital pit. Unfortunately, this pit is very shallow and frequently difficult to distinguish. Among the larger “hornless” ruminants, the female cervids sometimes possess small upper canines, whereas the antilocaprids and bovids never do. The cervids always have a rostral fenestra and an antorbital pit. The antorbital pit is always lacking in the Antilocapridae. However, the Bovidae may have both the fenestra and the pit, one of these structures, or neither of them.

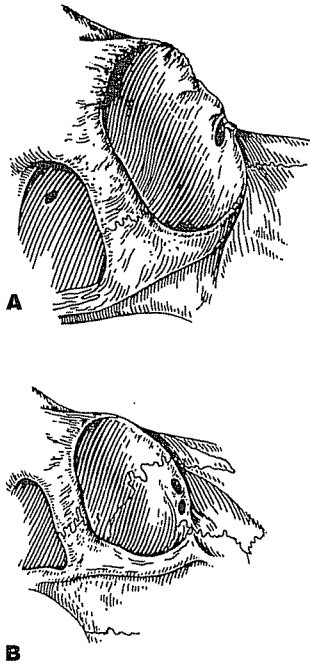


Figure 27.19 Orbital regions of the skulls of a bovid, Bovidae (A) and of a cervid, Cervidae (B). Cervids have a double lacrimal orifice in the orbit, whereas most bovids have a single orifice.

(Gromov et al. 1963)