



## Part I

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# Hoofed Mammals: Antelopes and Other Ruminants

## Order Artiodactyla

True ungulates are hoofed mammals that walk on tiptoe. They are classified in 2 different orders, Perissodactyla and Artiodactyla, depending on whether they have an odd (Gr. *perisso-*) or even (Gr. *artio-*) number of toes (*dactyla*). In artiodactyls the axis of the foot passes between digits 3 and 4; in perissodactyls (zebras, rhinoceroses, tapirs) it passes through the third, middle digit. The early artiodactyls had 4 hooves (digits 2 to 5), a condition that persists in hippos and pigs. The number has been reduced to 1 pair in the ruminants, but the vestiges of digits 2 and 5 are still present as the false hooves (2, 3).

Of the approximately 200 different kinds of recent hoofed mammals, all but 17 are artiodactyls, and of these all but 20 are ruminants (suborder Ruminantia). The 20 non-ruminants include the pigs and hippos, and the camelids (suborder Tylopoda). The latter are only distantly related to other artiodactyls, having separated in the Eocene and later developed a ruminating digestive system that differs in important respects from that of the true ruminants (1, 2). The camels that live in Africa descend from domesticated livestock introduced from Asia and therefore are not considered further in this *Guide*.

### References

1. Janis and Jarman 1984.
2. Romer 1959.
3. Young 1962.





# Introduction to the Ruminants

## Suborder Ruminantia

Family	Distribution center	African species
Tragulidae (chevrotains)	Southeast Asia	1
Giraffidae (Giraffe, okapi)	Africa	2
Cervidae (deer)	Old and New World temperate zone	1 (North Africa)
Bovidae (antelopes, sheep, goats, cattle)	Africa and Asia	75

**TRAITS.** Even-toed ungulates that chew the cud, ranging in size from the 1.5 kg royal antelope to a 1900 kg giraffe. *Teeth:* upper incisors absent, lower incisors augmented by incisiform canines to make a row of 8 chisel-shaped teeth; upper canines absent or vestigial except in chevrotains and primitive deer; cheek teeth complexly folded and sharply ridged, adapted for grinding, 2 or 3 premolars and 3 molars in each quadrant.

**ANCESTRY.** During the Eocene, while perissodactyls were diversifying and getting bigger, artiodactyls remained small (< 5 kg) forest frugivores and omnivores (table 1.1). But some 37 million years ago, the formerly subtropical global climate turned cooler, leading to seasonal rather than perennial production of fruits and nonfibrous vegetation. In the process of adapting to the new regime, artiodactyls became bigger and some specialized as herbivores. Pigs, camels, and ruminants were all established by the Oligocene. Ruminants reached Africa from Eurasia c. 24 million years ago in the early Miocene (7). During the same epoch, grasslands began to spread, replacing subtropical woodlands with more open savanna, and ruminants, with their superior ability to digest a fibrous diet (see chap. 2), likewise spread and diversified, becoming the dominant large herbivores.

The latest and most successful ungulate radiation was by the hollow-horned ruminants, the Bovidae. In Africa all but 3 of the

Table 1.1 Geologic Time Scale of the Cenozoic Era, the Age of Mammals

Period	Epoch	Ma <sup>a</sup>	Major events
QUATERNARY	Pleistocene	1.6	Ice Ages; early man; Golden Age of Mammals: maximum no. species, giant forms, followed by extinctions = 40% of species in last 20–10,000 yrs.
TERTIARY	Pliocene	5	Giraffe, warthog, zebras, camel, elephant. <i>Homo erectus</i> and existing genera of bovids and carnivores appear in late Pliocene-early Pleistocene
	Miocene	24	Early rhinos, aardvark. Ruminants become dominant as grassland habitats spread. <i>Australopithecus</i> in Miocene-Pliocene boundary
	Oligocene	37	Hyrax radiation, giraffe and elephant progenitors, early carnivores, first apes, cercopithecoid monkeys
	Eocene	58	Dominance of large archaic forms, replaced in late Eocene and early Oligocene by varied, mostly small ancestors of modern mammals
	Paleocene	65	Various existing and extinct orders (e.g., creodont carnivores) arise from primitive insectivore stock and diversify
CRETACEOUS			Age of Reptiles

<sup>a</sup>Millions of years ago.

living ruminants belong to this family. Accordingly Part I is mainly about bovids and, in particular, about antelopes.

### ADVANTAGES AND DISADVANTAGES OF RUMINANT DIGESTION.

A key advantage of the ruminant's digestive system is its superior ability to convert cellulose, the main constituent of all plant tissues and fibers, into digestible carbohydrates. Actually, all herbivores and even omnivores share this ability in some degree, including monkeys and plant-eating carnivores. The breakdown is accomplished not by the animal itself but by symbiotic microorganisms that digest cellulose by fermentation (4). In nonruminants fermentation occurs in the large intestine and an adjacent pouch, the cecum (of which our appendix is a vestige), *after* the food has passed through the stomach. In ruminants, fermentation takes place *before* gastric digestion, mainly in the rumen (fig. 1.1). Much more fiber is left undigested in the former system, as can readily be seen by comparing the coarse dung of a zebra, rhino, or elephant with the fine-grained dung of any ruminant.

The rumination process is both mechanically and biochemically complex and still not fully understood. First the animal feeds until the rumen is comfortably full, gripping foliage or grass between its lower incisors and upper dentary pad, plucking, and then

swallowing after briefly chewing each mouthful. Then it settles down to ruminate, either lying or standing, chewing the cud with rhythmic side-to-side jaw movements.

The cud consists of the coarsest plant particles, which float on top of the semiliquid rumen contents and are regurgitated a mouthful at a time through contractions of the rumen and its annex, the reticulum (the "honeycomb tripe" relished by some gourmets). As the ruminant grinds each mouthful at a steady rate, on the same or alternate sides of the mouth, enlarged salivary glands secrete a buffered solution that helps to maintain the rumen pH preferred by the resident microorganisms. Grinding the food promotes the full extraction of nutrients by increasing the surface area that is exposed to bacterial action. Some nutrients are absorbed through the rumen wall, which is lined with tongue- or finger-shaped papillae; these both vastly increase the absorptive area and provide cranies in which bacteria and protozoans multiply.

Rhythmic contractions of the rumen and reticulum keep stirring the "vat," sorting food particles according to size and specific gravity. The smallest particles sink to the bottom, and from there are pumped through the reticulum into the omasum (fig. 1.1), also known as the "book organ" or "psalter" because of the leaflike plates that line it. Here the semiliquid ingesta are filtered once more before being pumped into the abomasum, the true stomach. Afterward, during passage through the intestines, the residue undergoes some final cellulose digestion in the cecum (4).

In addition to the more complete utilization of plant fiber in ruminant digestion, the constantly reproducing and dying rumen microorganisms that do the work provide the host with energy in the form of volatile fatty acids they excrete as metabolic wastes, and the organisms themselves become a major source of protein as they pass through the digestive tract mixed together with the rumen contents (2, 4). Ruminants possess the further important advantage of being able to recycle urea, thereby retaining and recycling inorganic nitrogen that the ruminant bacteria use to reproduce and to synthesize more protein. From this bacterial protein ruminants acquire the essential amino acids that nonruminants have to gain from their plant food. As an added bonus, recycling urea cuts down on urine excretion, helping to conserve water and contributing to the water-indepen-

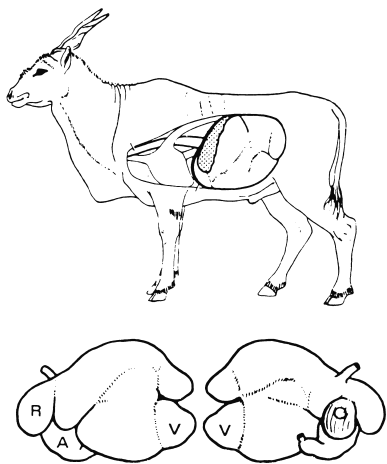


Fig. 1.1. The ruminant stomach. *Top*: an eland's rumen shown in situ, overlain by the spleen (dotted organ). *Bottom*: an eland's stomach in left and right aspect: R, reticulum; A, abomasum; O, omasum; V, ventral blind sac. The rest is the rumen. (From Hofmann 1973.)

dence of desert-adapted ruminants (chap. 2) (7).

There is 1 major drawback to rumination: the thorough digestion of cellulose takes time, and the more fibrous the food the longer the process. It can take up to 4 days from ingestion to excretion. When protein content falls below 6 percent, ruminants cannot process their food fast enough to maintain their weight and condition (4, 7, 8). Hindgut fermenters consume and partially digest large quantities of low quality forage in half the time; they can thereby manage to obtain adequate sustenance from vegetation too tough and fibrous for ruminants to process. Thus, a horse can extract only  $\frac{2}{3}$  as much protein from a given quantity of herbage as a cow, but by processing twice as much in a given time, its assimilation of protein will exceed the cow's by  $\frac{1}{3}$  times.

Supposedly, ruminants are also less efficient than nonruminants at digesting fruits, because predigestive fermentation removes fruit sugars and other nutrients that would otherwise be digested and absorbed in the true stomach (7). Nevertheless, most small forest ruminants are largely frugivorous, and even some of the larger duikers have diets consisting of over 70 percent fruit (see below).

#### **Behavior Associated with Rumination.**

All ruminants except chevrotains lie down by first kneeling on their forelegs (carpal joints), then lowering the rear end. They rise in reverse order, raising the rear end first. To enable the stomach compartments to move freely, ruminants have to lie on the brisket or stand while ruminating. They rarely lie on their sides for more than a few minutes at a time, and rolling on the back is unheard of (but see wildebeest

accounts). If anesthetized ruminants are left lying on their sides, they are likely to ingest rumen contents and suffocate. Ruminants doze but do not sleep soundly like nonruminants. Possibly the need to maintain a certain position and to keep chewing the cud precludes normal sleep. Yet rumination goes together with a relaxed state (the "contented cow") and, significantly enough, the brain waves of ruminating animals resemble those associated with sleep in nonruminants (1).

#### **RESOURCE PARTITIONING**

**AMONG AFRICAN RUMINANTS.** Ruminants that live on fruit and soft, succulent vegetation high in protein and low in fiber have a small, comparatively simple rumen that recalls its origin as an S-shaped tubular blind sac serving initially merely as a food storage chamber (5).

Chevrotains, the most primitive living ruminants, have only a 3-chambered stomach (no omasum). The digestive system is most completely differentiated and complex in the grazing ruminants such as cattle, sheep, wildebeest, and oryx.

Ruminants of the second type are usually classified as *grazers*; those that eat fruit and foliage are lumped together as *browsers*. But these designations oversimplify and obscure the range of differences within each group and exclude those intermediate feeders that both browse and graze. After studying and comparing the stomach morphology of 29 wild ruminants of East Africa, Hofmann (5) proposed the following classification:

1. Concentrate selectors
  - a. Fruit and dicotyledon foliage selectors: duikers, dikdiks, suni, klipspringer, bushbuck, and other (mostly small) ruminants of bush and forest
  - b. Tree and shrub foliage eaters: giraffe, renyek, lesser and greater kudu, and other medium to large browsers of savanna and bush habitats
2. Bulk and roughage eaters
  - a. Fresh-grass, water-dependent grazers: reedbuck, kob, waterbuck, wildebeest, buffalo
  - b. Roughage grazers: hartebeest, topi, mountain reedbuck
  - c. Arid-region grazers: oryx
3. Intermediate (mixed) feeders
  - a. Predominantly grass (grazer/browsers): impala, Thomson's gazelle
  - b. Predominantly forbs, shrub or tree foliage (browser/grazers): eland, Grant's gazelle, steenbok

The small, simple stomach of concentrate selectors is designed for the quick



**Fig. 1.2.** An eland bull chewing its cud, lying on the sternum in the usual ruminating position.

fermentation and absorption of food rich in protein, fat, and nonfibrous carbohydrate. Ruminants in class 1a are extremely selective feeders that choose food items of the highest protein content. They feed in many short bouts, rarely filling the rumen more than half full before pausing to ruminate. The rumen contents are not stratified as in roughage feeders, and concentrate feeders generally obtain enough moisture from their food without needing to go to water. But larger (1b) species need to put away more food to sustain their greater bulk and therefore cannot afford to be as choosy. To process bulkier but still easily fermented foliage, they have larger, more subdivided stomachs designed to slow food movement and allow more time for fermentation.

Grazers have the greatest ability to subsist on vegetation that is relatively low in protein and high in fiber. A large capacity combined with food-delaying mechanisms is characteristic. The different stomach chambers are more muscular and subdivided, functioning to churn, pump, sieve, and filter the ingesta. The omasum, in particular, which is merely a strainer in concentrate selectors, is highly developed and serves a new and essential function as a site where water and soluble nutrients are absorbed. Grazers keep eating until the rumen is full, regardless of grass quality, then settle down for a long rumination bout (6–8 hours).

Roughage grazers (2b) can subsist on pastures with low nutrient availability, partly because they are equipped to feed more selectively than most bulk grazers. A relatively smaller capacity and reduced absorptive area are adaptations for a low-energy diet (6). The 3 antelopes listed in this category can go for long periods without drinking. However, the oryx is the only predominantly grass-eating ruminant in Hofmann's sample that is adapted to extremely arid conditions without surface water.

Mixed feeders have a greater ability to adapt to different habitats and seasonal vegetation changes than either concentrate selectors or grazers. When grasses are green and tender they graze, and when pastures become mature and tough or dry into hay they switch to foliage. These changes are accompanied by changes in stomach structure that reduce or enlarge the mucosal surface that is available for absorption, and also by changes in the microorganisms that are adapted to ferment the different types of plants. The basic stomach plan is similar to concentrate selectors. An animal that has adapted for a concentrate diet can-

not begin digesting grass without making a gradual transition, and vice versa.

The extraordinary versatility of the ruminant stomach helps to explain how the ruminants could become so diverse, filling a greater variety of ecological niches than any other group of herbivores. The ability to structure the digestive system precisely for a given diet has enabled ruminants to partition African ecosystems into much narrower feeding niches than can nonruminants, which require a greater variety and amount of vegetation to meet their nutritional needs (7).

### ECOLOGICAL SEPARATION BY

**SIZE.** Obviously size and shape are closely connected with where and how an animal lives and what it eats (2, 8, 9). As discussed in chapter 2, the transition from concentrate selectors living in closed habitats to roughage grazers of open savanna is correlated with increasing size. But how intimately size can be connected with habitat has been revealed only recently by studies of rain-forest ruminants in Gabon. Dubost (3) found that the structure of the undergrowth predetermines shoulder heights within very precise limits. Instead of the wide spread in sizes that would be expected, the shoulder heights of 9 sympatric species clustered at a few different points: 35–40 cm (water chevrotain and blue duiker); 50–55 cm (Peter's, bay, and black-fronted duikers); 75–80 cm (yellow-backed duiker); 90–95 cm (bushbuck); and 115–125 cm (buffalo and bongo). Four of these 5 height classes turned out to be levels at which the vegetation offered least obstruction to passage in the form of horizontal and diagonal branches at chest height. Only the 2 smallest species proved to be in a disadvantageous height class. The blue duiker avoids the problem by living in places with very little undergrowth (see species account), whereas the chevrotain has a piglike shape and thickened dorsal skin that enable it to force its way through the densest thickets. Two other associated artiodactyls, the bushpig and giant forest hog, have a similar build and are also not size-limited by the vegetation structure. But most ruminants, with their light build and other adaptations for rapid flight, are very sensitive to their physical environment (3).

### References

1. Bell 1971.
2. Demment and Van Soest 1985.
3. Dubost 1979.
4. Dukes 1955.
5. Hofmann 1968.
6. ——— 1973.
7. Janis and Jarman 1984.
8. McNaughton and Georgiadis 1986.
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# Antelopes and Buffalo

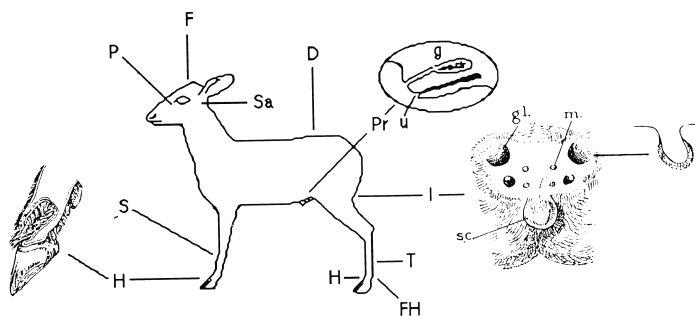
## Family Bovidae

Tribe	African genera	African species
Cephalophini: duikers	2	16
Neotragini: pygmy antelopes (dik-dik, suni, royal antelope, klipspringer, oribi)	6	13
Antilopini: gazelles, springbok, gerenuk	4	12
Reduncini: reedbuck, kob, waterbuck, lechwe	2	8
Peleini: Vaal rhebok	1	1
Hippotragini: horse antelopes (roan, sable, oryx, addax)	3	5
Alcelaphini: hartebeest, hirola, topi, blesbok, wildebeest	3	7
Aepycerotini: impala	1	1
Tragelaphini: spiral-horned antelopes (bushbuck, sitatunga, nyala, kudu, bongo, eland)	1	9
Bovini: buffalo, cattle	1	1
Caprini: ibex, Barbary sheep	2	2
Total	26	75

**FAMILY TRAITS.** Horns borne by males of all species and by females in 43

of the 75 African species. *Size range:* from 1.5 kg and 20 cm high (royal antelope) to 350 kg and 178 cm (eland); maximum weight in family, 1200 kg (Asian water buffalo, *Bubalus bubalis*); maximum height: 200 cm (gaur, *Bos gaurus*). *Teeth:* 30 or 32 total (see chap. 1, Ruminant Traits). *Coloration:* from off-white (Arabian oryx) to black (buffalo, black wildebeest) but mainly shades of brown; cryptic and disruptive in solitary species to revealing with bold, distinctive markings in herding plains species. *Eyes:* laterally placed with horizontally elongated pupils (providing good rear view). *Scent glands* (fig. 2.1): developed (at least in males) in most species, diffuse or absent in a few (kob, waterbuck, bovines). *Mammæ:* 1 or 2 pairs.

**Horns.** True horns consist of an outer sheath composed mainly of keratin over a bony core of the same shape which grows from the frontal bones. Keratin, a tough, horny substance, is also the main constituent of hooves, nails, claws, hair, scales, and feathers. Horns grow slowly from an



**Fig. 2.1.** Outline drawing of an antelope, showing locations of scent glands. *H*, hoof (interdigital) gland of a wildebeest; insert shows forefoot with one side cut away, exposing the flask-shaped gland between the digits. *S*, shin (carpal) gland (gazelles). *P*, preorbital gland (see fig. 4.1). *F*, glandular skin (impala). *Sa*, subauricular gland (reedbucks, oribi). *D*, dorsal gland (springbok). *I*, inguinal glands. Inset of reedbuck inguinal area: *gl*, gland orifice (cross-section shown in inset); *m*, mammary; *sc*, scrotum. *T*, metatarsal gland (impala only). *FH*, false-hoof gland (see fig. 9.1). *Pr*, preputial gland (inset: *g*, glandular sac; *u*, opening of penile sheath). (Inset drawings from Pocock 1910, 1918.)

epidermal layer surrounding the bony core and if broken or cut off do not regenerate. They are never branched or shed like deer antlers, which are made of solid bone. Horns evolved before hair, first in the dinosaurs, later in rhinoceroses, and at least 3 times in different families of ruminant artiodactyls. But the structural plan of bovid horns is unique to this family (18).

Horns are the weapons with which males of all species compete for dominance and reproductive success (22). Horns are present in the females of 43 African species, but are generally smaller and invariably thinner and weaker (27), reflecting the absence of sexual competition that subjects males' horns to rigorous testing in combat. There is growing fossil evidence that horns evolved first in males, and only later in females of different lineages and at different times (17, 18, E. Verba, pers. comm.). The conventional view of female horns is that they evolved as weapons of self-defense (27). But according to my own theory (10), females of polygynous species evolved horns to mimic the horns of their male offspring as a way of reducing harassment of adolescents by mature males, which leads to their separation from female herds with consequent higher mortality. When horns are present in both sexes, they cease to be badges of maleness and so young males are less likely to be singled out until they cease to resemble females. In species such as oryxes and wildebeests, the resemblance continues into adulthood and facilitates the formation of mixed herds in these migratory/nomadic antelopes. Thus, although females of all horned species surely do use their horns as weapons, in my view this is a secondary or derived function.

Like other male secondary sex characters, horns are the products of sexual selection (2) and the degree of development reflects the degree of male competition. Thus, horns are no more than simple spikes in the monogamous duikers and dwarf antelopes, but huge and elaborate in many of the highly polygynous species like the impala, sable, greater kudu, goats, and sheep.

**DISTRIBUTION.** Africa is the land of antelopes. Wherever vegetation grows, one species or another has adapted to eat it, from the depths of the Sahara, where the endangered addax formerly held sway, to the depths of the Equatorial Rain Forest, where duikers live; from swamps (sitatunga and lechwe) to the Afro-Alpine Biome (bushbuck, eland, duikers). Seventy-two of the 75 bovids are antelopes. The African buffalo

falo is the only bovine that occurs naturally in the Ethiopian Faunal Region. Sheep and goats, which belong to the Eurasian fauna, have 2 African representatives, the aoudad or Barbary sheep (*Ammotragus leervia*) and the ibex (*Capra ibex*); they range as far south as the Sahel and the Abyssinian Highlands.

Only two tribes of African antelopes occur outside the continent: the Antilopini, with 9 out of a total of only 12 Asian antelopes, and the Arabian oryx (*Oryx leucorox*) which gives the Hippotragini a foothold on the Arabian Peninsula.

What exactly is an antelope? Technically, it is the name of the Indian blackbuck, *Antelope cervicapra*, and applies to the members of its tribe, the Antilopini. In practice, bovids of all tribes apart from cattle (Bovini), sheep and goats (Caprini), and goat-antelopes (Rupicaprini) are called antelopes. But in fact, antelopes from different tribes are as unlike as are sheep and cattle. The 9 tribes of African antelopes thus represent a diversity of bovids far greater than on any other continent, either now or in the past.

### THE AFRICAN BOVID RADIATION.

The extraordinary diversity of African antelopes can be attributed to a number of interconnected factors (3, 18, 20, 25).

1. The African continent is unusually large and physiographically diverse. It has by far the largest tropical land mass, being the only continent that spans both tropics. The great variety of life zones (biomes) that presently exist began to differentiate during the middle Miocene, providing new and shifting ecological opportunities for the bovids to exploit. (See table 1.1.)

2. The bovid array represents the most recent ungulate radiation, which reached its peak within the last several million years in the Pliocene and Pleistocene. Although Africa, like the other continents, had its share of Pleistocene extinctions, most of the genera and species of antelopes that ever existed are still with us (14).

3. The African fauna has been repeatedly enriched by immigrations from Eurasia during extended periods when land bridges connected the 2 continents (24). The earliest known bovid, the gazelle-sized *Eotragus*, occurred both in Europe and North Africa 20 million years ago. By the late Miocene, African bovids had diversified into 9 distinct tribes, but most had Asian relatives. A massive invasion of Asian genera in the early Pliocene, followed by differentiation of African types, resulted in a major faunal rev-



olution: over 85% of the Pliocene genera are new, including 19 genera of bovids, of which all but 5 are unknown outside Africa. As late as the early Pleistocene, new genera continue to appear in the fossil record, due both to Asian immigrants (8 more bovid genera) and *in situ* evolution. The duikers, neotragines, and reedbuck/kobs are the only bovid tribes that evolved in Africa and never reached Asia (22, 24).

4. The Sahara Desert has imposed a formidable barrier to intercontinental movement since the second half of the Pleistocene, as reflected by a much higher proportion of endemic African mammals. Eurasian species could still disperse to North Africa but only desert-adapted forms could penetrate the Sahara. Most of the Eurasian tropical-savanna fauna proceeded to become extinct during the Ice Age, leaving Africa as the final refuge of Plio-Pleistocene mammals (24).

5. Speciation within Africa was promoted by expansion and contraction of the Equatorial Rain Forest during wet (pluvial) and dry (interpluvial) periods of the Ice Age. During pluvial periods the rain forest stretched from coast to coast, barring interchange between northern and southern savanna and arid biomes but facilitating the dispersal of forest forms. In succeeding interpluvials the rain forest was reduced to a number of isolated islands, and a drought corridor extending through eastern Africa connected the savanna and arid biomes; this explains the presence of some of the same mammals in the Somali and South West Arid Zones, separated by the whole *Miombo* Woodland Zone (see vegetation map), for instance the oryx, dik-dik, steenbok, bat-eared fox, and springhare (*Pedetes capensis*) (22).

6. A fundamental reason for the great diversity and success of the bovids is their ability to specialize more narrowly and efficiently than other ungulates. By tailoring size, feeding apparatus, digestive system, and dispersion pattern for a particular set of ecological conditions, antelopes have effectively partitioned African ecosystems into many small segments (see chap. 1 and refs. 3, 22, 25).

**Tribal Niches.** A commitment to one type of biome or another is seen in most of the tribes and genera and presumably dates back to the original differentiation of tribes in the Miocene and Pliocene.

- Gazelles and other Antilopini are specialized for arid biomes; they are medium-sized, wide-ranging gleaners which can subsist in areas too dry and poor to support

larger roughage eaters. A *Gazella* species was roaming the Kenya plains 14 million years ago (14).

- The neotragines are small antelopes, allied to the gazelles, that lead sedentary, solitary lives within various closed habitats, from rain forest to subdesert.

- The duikers are specialized as forest fruit- and foliage-eaters.

- Members of the bushbuck tribe are medium and large browsers that inhabit mostly closed habitats, from forest to subdesert thornbush.

The remaining 4 tribes are grazers that have specialized for different grassland habitats.

- Cattle and the reduncines live in valley and floodplain grasslands within a short distance of water.

- Alcelaphines disperse into dry savanna during the rainy part of the year and concentrate on greenbelts near water points in the dry season (9).

- Hippotragines include the desert-adapted addax and oryx as well as the water-dependent sable and roan, which inhabit the well-watered savanna woodlands (1, 5). These ecological specializations are considered in more detail in the tribal introductions and species accounts.

**PHYSIOLOGICAL ADAPTATIONS FOR ARID CONDITIONS.** Vast regions of Africa and Asia are uninhabitable or only seasonally habitable by animals dependent on drinking water. Bovids able to obtain all the water they need from their food can exploit the vegetation of arid lands and thereby avoid the more rigorous competition for plants within commuting distance of water. Browsers in general are less water-dependent than grazers, mainly because bushes and trees can reach down to moist soil and produce green growth at times when grasses are parched. Moreover, many plants of arid and semiarid environments have water-storage organs such as thickened roots and tubers or succulent stems and leaves. Parts of the Kalahari sandveld produce such an abundance of melons and tubers that even water-dependent grazers like the wildebeest and hartebeest are able to live there without surface water. However, antelopes such as most gazelles, oryxes, and dik-diks require less water to survive, especially when it is extremely dry and hot. The key physiological adaptations include:

1. Allowing body temperature to rise
2. Lowered metabolic rate, decreasing with dehydration

- 3. Reflecting coat: flat, dense, short, smooth, light color (11)
- 4. Concentrating urine; extracting moisture from feces
- 5. Nasal panting and cooling of the blood to avoid overheating

Allowing body temperature to rise with environmental temperature—by as much as 10°C—is the most important water-conservation measure, one that is also employed by camels (29, 30). Desert-adapted species can let their body temperature go higher for longer than can other antelopes. To maintain a constant body temperature on a hot day requires water for evaporative cooling, even though the common bovid technique of closed-mouth panting is much less wasteful than sweating. Air passed across the nasal mucosa while breathing rapidly cools the blood by evaporating moisture from the nasal mucosa. The cooled venous blood then flows through a capillary network (the *rete mirabile*) surrounding the carotid arteries, where it cools the blood going to the brain (29).

**CORRELATIONS BETWEEN HABITAT PREFERENCE, MORPHOLOGY, ANTIPREDATOR STRATEGY, AND SOCIAL ORGANIZATION.** An analysis of the 75 species of African bovids indicates that habitat preferences, diet, size,

conformation, gaits, coloration, antipredator strategy, degree of sexual dimorphism, mating system, and social organization are all coadapted (9). In table 2.1 a basic dichotomy in the traits of solitary and gregarious species is demonstrated by the results of a series of correlation tests. The significance of these differences is illustrated by comparing the traits of forest duikers, representing solitary antelopes adapted for closed habitats, with the adaptations of an oryx, an advanced open-country antelope (table 2.2).

The duikers' conformation, short, slanted horns, and gaits are designed for movement through and under dense vegetation, often on soft ground (hence the splayed hooves). The presence of undergrowth, intimate knowledge of a small home range, small to medium size, cryptic coloration, and solitary habits all support a concealment strategy. The oryx's build and gaits are adapted to traveling long distances across arid, often hard ground (hence the compact hooves). Fleet and enduring, big, well-armed and aggressive, the oryx is well-equipped to escape, and even defend itself against, predators. Although the newborn are concealed, adults avoid heavy cover. Water-independence enables the oryx to reside in arid regions that are permanently or seasonally beyond reach of water-dependent species.

Table 2.1 Correlations Between Social Organization and Selected Traits of the 75 Species of African Bovidae

	Solitary	Gregarious	$\chi^2$
Total number of species	32	43	
Habitat preference			
Closed	30	9	
Open	2	34	38.98
Diet			
Browse or mixed (browse and grass)	31 <sup>a</sup>	21	
Primarily grass	3 <sup>a</sup>	20	10.98
Size			
Small to medium (1.5–45 kg)	28	10	
Medium to large (45–950 kg)	4	33	30.29
Conformation			
Rounded back, massive hindquarters, short legs	31	12	
Cursorial (long legs, back level or high shoulders)	1	31	32.91
Coloration			
Concealing (cryptic or disruptive)	31	12	
Revealing (contrasting color and/or markings)	1	31	32.91
Male horns			
Primitive: short, straight spikes or forward hooks	30	3	
Advanced: medium to large size or complex shape	2	40	52.60
Sexual dimorphism (in body size, horns, coloration, or other male secondary characters)			
Minimal	29	13	
Pronounced	3	30	27.16
Antipredator strategy of adults			
Concealment or flight to cover/sanctuary	32	13	
Avoid cover and flight in open	0	30	32.16

NOTE: All the chi-square values are highly significant ( $P < .010$ , 1 df).  
<sup>a</sup>Includes 4 of the least sociable gregarious species: gerenuk, dibatag, mountain reedbuck, and sitatunga.

**Table 2.2 Comparison of a Solitary Forest Antelope with a Gregarious Plains Antelope**

	Forest species	Plains species
Species	Forest duiker	Oryx
Biome	Lowland and montane forest	Arid zones
Size	Small to medium (4.5–64 kg), female slightly larger than male	135–205 kg, male larger than female
Horns	Both sexes, short (5–25 cm) spikes	Both sexes, long (up to 120 cm), straight or curved
Conformation	Hindquarters more developed than forequarters, back rounded, legs short, hooves with wide splay	Limbs equally developed, back level, legs long, hooves with little splay
Gaits	Walk: cross-walk Trot: rarely observed Run: dodging, interspersed with flat leaps, head and neck low	Walk: amble Trot: long, ground-gaining Run: a fast, horselike gallop, head at shoulder level or above
Preorbital glands	Well-developed in both sexes	Vestigial or absent
Feeding habits	Concentrate selectors	Roughage feeders
Water metabolism	Water-dependent (?)	Water-independent
Coloration	Concealing	Revealing (except calves)
Social system	Solitary or monogamous, sedentary, small home range/territory	Gregarious, polygynous, nomadic, $\pm$ territorial, mixed herds and solitary males, huge home range
Breeding	Perennial; females and males mature at 1–2 years	Seasonal; females mature at 3, males at 4–5 years
Offspring	Concealed	Concealed, or calves join together in crèches
Reaction to danger	Take cover and hide	Flee in open

Group formation is a basic adaptation to life in the open; the oryx goes further and lives in mixed herds, apparently as a specialization for a subdesert biome where overall population density is very low. The long, straight horns and conspicuous markings serve as species-recognition characters that make an oryx unmistakable for any other animal.

**Mating System, Age at Maturation, and Sexual Dimorphism.** Sexual dimorphism in bovids, as in most mammals, is the result of male reproductive competition, which causes males to acquire physical and behavioral traits that enhance their ability to compete successfully. The greater the potential reproductive success, that is, the more females with which a male may mate—the more polygynous—the greater the sexual competition and the greater the degree of sexual dimorphism that is likely to develop (6, 10, 15, 20). The different types of social organization and mating systems are considered below.

In a monogamous system, with only one female for each male, male sexual competition is minimal and consequently there is little dimorphism—the sexes look much alike (unimorphic or unisex). In fact, females tend to be slightly larger than males in the duikers and dwarf antelopes. In all the other tribes, males mature later

and end up larger than the females. The degree of size dimorphism within a species increases with the difference in age at maturation; it is much greater in species where males mature 3 or 4 years later than females than when the difference is only 1 or 2 years. This helps to explain why the most pronounced dimorphism occurs in bovids of medium and large size, for development takes longer than for smaller species (10, 15, 20, 25). Dimorphism is particularly developed in the Reduncini (kob, lechwe) and Tragelaphini (nyala, sitatunga, kudu, eland).

But the sexes look much alike in the Alcelaphini and Hippotragini, which include 8 of the 18 most gregarious antelopes. These species, though polygynous, share the tendency to form mixed herds containing adults of both sexes. Sexual segregation, conversely, increases with increasing sexual dimorphism. The correlation between these tendencies in the 43 gregarious African bovids is highly significant (table 2.3). Apparently selection for uniformity exists in species like oryx and wildebeest that are under ecological pressure to integrate, and counteracts selection for sexual dimorphism (10, 13).

Concerning the forms of sexual dimorphism, contrasts in horn development are of-