

# MORPHOLOGY OF HORNS AND FIGHTING BEHAVIOR IN THE FAMILY BOVIDAE

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Horns of bovids are remarkably diverse. This diversity may reflect functional differences associated with the use of horns as intraspecific weapons. I use measurements from museum specimens and behavioral data from the literature to examine the relationship between morphology of horns of males and fighting behavior in 21 species of bovids, representing 11 of the 12 bovid tribes. A high correlation between morphology of horns and fighting behavior was found. In particular, a short horn reach and undeveloped catching arch is associated with stabbing behavior; a long horn reach, with wrestling and fencing behavior; a well-developed catching arch, with wrestling behavior; and robust, recurved horns, with ramming behavior. A phylogeny of bovid tribes suggests that these features of morphology of horns and fighting behavior are rapidly evolving and frequently convergent.

**Key words:** Bovidae, horns, morphology, fighting behavior

Bovidae (goats, sheep, cattle, buffalo, bison, and antelope) is a large and diverse family, currently represented by 45 genera and 137 species (Grubb, 1993). The majority of extant bovids occur in Africa (79 species), but wild bovids also are found in Eurasia and North America.

The most distinctive characteristic of bovids is their paired frontal horns, which are permanent and present in males of all species of bovids. Although horn-like structures occur throughout the animal kingdom, true horns, with a bony core surrounded by a sheath of cornified epithelium, are exclusive to the family Bovidae (Goss, 1983).

The function of horns of bovids has long been debated. In the early 19th century, most biologists believed that horns functioned primarily as anti-predator weapons. There are many examples of the use of horns as anti-predator weapons, particularly among species that show active group defense (e.g., African buffalo, *Syncerus caffer*—Makacha and Schaller, 1969; Sinclair, 1977; eland, *Taurotragus oryx*—J. C. Hillman, in litt.; Kruuk, 1972; muskox, *Ovibos moschatus*—Tener, 1965). However, most bovids flee from predators and rarely are

observed using their horns as anti-predator weapons. A great diversity of types of horns are found among species inhabiting the same region, and in ca. 30% of extant species, females do not possess horns. These observations suggest that the need to defend against predators has not been the primary selective force in the evolution of horns in bovids.

Darwin (1871) was the first to suggest that horns evolved in the context of sexual selection as weapons of male-male competition. There is ample evidence that male bovids use their horns in intraspecific combat. Males that win fights obtain a territory (e.g., kob, *Kobus kob*—Buechner and Roth, 1974; Coke's hartebeest, *Alcelaphus buselaphus cokei*—Gosling, 1974) or dominance in a mixed-sex herd (e.g., African buffalo—J. J. R. Grimsdell, in litt.; mountain sheep, *Ovis canadensis*—Geist, 1966, 1971), and thus, gain access to females in estrus. Although the relationship between fighting success and lifetime reproductive success has not been measured in any bovid, Clutton-Brock et al. (1982) demonstrated that fighting ability in red deer (*Cervus elaphus*, family Cervidae) is positively cor-

related with lifetime reproductive success. It seems likely that a similar relationship applies for bovids and the importance of intraspecific combat in the evolution of horns is now generally accepted (Geist, 1966; Janis, 1982; Leuthold, 1977; Packer, 1983; Walther, 1966).

However, if horns evolved primarily in the context of male-male competition, why have so many different types of horns evolved? Horns of bovids are remarkably diverse; indeed, interspecific variation is so pronounced that most species are easily recognized by the characteristic shape of horns of males.

The most compelling explanation is that interspecific differences in morphology of horns reflect differences in fighting behavior. Geist (1966) recognized three stages in the evolution of shape of horns, each roughly associated with a particular fighting style. The first stage is represented by species with small, spike-like horns. Combatants stand parallel or anti-parallel to one another; during fights, piercing blows are aimed at the opponent's flank or belly. This fighting style is associated with an inhibition to strike, presumably because the potential for serious injury is high. The second stage is represented by species with larger, more complex horns; blows are still aimed at the opponent's flank or belly, but because the horns are used defensively (i.e., to catch blows) as well as offensively, orientation is usually head to head. The most "advanced" stage is represented by two distinct types in which the head itself is usually the primary target, "rammers" and "wrestlers." Rammers possess massive horns; opponents charge at one another from a distance and collide head-on with great force. Wrestlers lock horns during fights, and combatants attempt to push or throw their opponent off balance.

Building on Geist's (1966) ideas, Schaffer and Reed (1972) collected data on morphology of skulls and horns for several species from the subfamily Caprinae (goats and sheep). They described a number of

morphological features that they associate with the evolution from the "primitive" fighting style of goat-antelopes (*Rupicapri*, Geist's stage 1) to the more "advanced" fighting style of true sheep (*Ovis*, Geist's stage 3, rammers). These include an increase in relative size of horns, an increase in curvature of horns, and an increase in the lateral compression of the core of the horn.

Kitchener (1985) conducted a more extensive examination of variation of horns, including representatives from 11 of the 12 bovid tribes (after Gentry, 1992). He hypothesized that changes in bending strength of horns, as indicated by  $I'$  (the second moment of area of the base of the horn, which is a fourth power function of the diameter at the base of the horn), would balance changes in bending stress imposed on horns during fighting (a function of both body weight and fighting style). To test this, he plotted  $I'$  against body weight for a large number of species and identified several groups of species where each group had a different positive linear relationship between the two variables. The different slopes of these regressions presumably reflect group-differences in fighting behavior. Species with more forceful fighting, such as sheep, have a larger diameter of base of the horn relative to body weight than those with less forceful fighting styles such as Neotragines.

Although some of Kitchener's (1985) groups are composed of species that share a similar morphology of horns and fighting style (e.g., "true sheep"), a wide variety of shapes of horns and fighting styles are represented in others (e.g., the "antelopes"). Intragroup variation in the latter probably reflects the fact that Kitchener's (1985) analysis considered only one aspect of morphology of horns (diameter at the base of the horn) and one aspect of fighting behavior (force of impact during ramming or clashing). In most species of bovids, fights involve a complex combination of elements (e.g., wrestling, stabbing, and ramming). Not all blows are delivered to the base of

TABLE 1.—Sample size (n) for the 21 species of bovids examined in this study (classification after Gentry, 1992).

Tribe	Genus and species	Common name	n
Tragelaphini	<i>Tragelaphus strepsiceros</i>	(greater kudu)	6
	<i>Taurotragus oryx</i>	(common eland)	15
Boselaphini	<i>Boselaphus tragocamelus</i>	(nilgai)	3
Bovini	<i>Syncerus caffer</i>	(African buffalo)	2
Cephalophini	<i>Cephalophus maxwelli</i>	(Maxwell's duiker)	7
	<i>Sylvicapra grimmia</i>	(common duiker)	21
Neotragini	<i>Neotragus batesi</i>	(pygmy antelope)	11
	<i>Oreotragus oreotragus</i>	(klipspringer)	9
Antilopini	<i>Gazella granti</i>	(Grant's gazelle)	21
	<i>Gazella thomsoni</i>	(Thomson's gazelle)	33
	<i>Litocranius walleri</i>	(gerenuk)	16
Reduncini	<i>Kobus ellipsiprymnus</i>	(waterbuck)	17
	<i>Kobus kob</i>	(kob)	9
	<i>Redunca arundinum</i>	(reedbuck)	18
Hippotragini	<i>Hippotragus niger</i>	(sable)	10
	<i>Oryx gazella</i>	(gemsbok)	10
Aepycerotini	<i>Aepyceros melampus</i>	(impala)	20
Alcelaphini	<i>Connochaetes taurinus</i>	(blue wildebeest)	15
	<i>Alcelaphus buselaphus</i>	(hartebeest)	23
Caprini	<i>Ovis canadensis</i>	(mountain sheep)	3
Indeterminate	<i>Oreamnos americanus</i>	(mountain goat)	4

the horn and important aspects of fighting (e.g., the ability to stab an opponent or hook his horns and throw him off balance) may not be significantly influenced by the diameter at the base of the horn.

Here I investigate the relationship between morphology of horns and fighting behavior in extant bovids, and evaluate the hypothesis that aspects of morphology and behavior have co-evolved. Because neither morphology of horns nor fighting behavior are adequately described by single variables, several measures of each are combined in a multivariate analysis. I have included, as measures of fighting behavior, the three primary components described in Geist's (1966) model; stabbing, ramming, and wrestling. Two additional measures, fencing and kneeling, were added to the analysis because they also are conspicuous and common components of fighting behavior of bovids.

#### MATERIALS AND METHODS

Morphological measurements were taken from skulls and horns of adult males from 21

species representing 11 of the 12 tribes (Table 1). Measurements of skulls included basal length (from the anteriormost point on the premaxillae to the ventral lip of the foramen magnum) and greatest breadth (measured perpendicular to the long axis of the skull).

The following measurements were taken from the sheath of the left horn: length along the anterior midline, circumference at the base of the horn, greatest reach (direct distance from the anterior midline at the base of the horn to the point farthest from it on the sheath of the horn), chord (direct distance from the anterior midline at the base of the horn to the tip of the horn), medio-lateral diameter at the base of the horn, and antero-posterior diameter at the base of the horn. For each individual, chord divided by length of the horn along the anterior midline was calculated as an indicator of straightness of the horn, and medio-lateral diameter at the base of the horn divided by antero-posterior diameter at the base of the horn was calculated as an indicator of the cross-sectional shape of the base of the horn (shape of base).

The left horn was divided into three functional zones (Fig. 1a): the stem (proximal straight element of the horn), stabbing zone (distal straight element of the horn), and catching arch

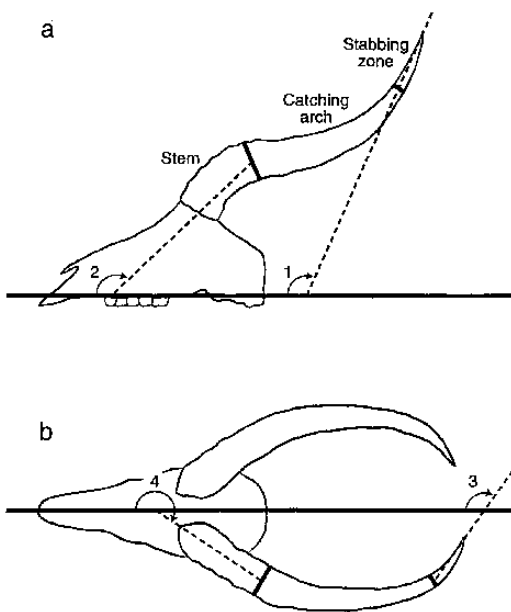


FIG. 1.—Diagram illustrating the three functional zones of the horn (stem, catching arch, and stabbing zone; modified after Kingdon, 1982), and four angles that reflect the orientation of the stem and stabbing zones with respect to palatal a) and mid-sagittal b) planes.

(the curved region between stem and stabbing zones; modified after Kingdon, 1982). These zones were defined by running a straight-edge along the midline of each of the two straight elements (the stem and stabbing zone) and marking on the horn the points where the straight-edge cleared the surface of the horn. The stabbing zone always was delineated first and was by definition the only zone present in species with perfectly straight horns. The length of each zone was measured along the anterior midline of the horn. The length of the catching arch divided by the length of the horn along the anterior midline was calculated as a measure of the percentage of the length of the horn occupied by the catching arch.

Photographs of each specimen were taken from two mutually orthogonal directions (from the left side and from above) and four angles were measured from tracings of the photographs (Figs. 1a and 1b). Angles 1 and 3 describe the orientation of the stabbing zone with respect to the palatal and mid-sagittal planes, respectively. Angles 2 and 4 describe the orientation of the

stem of the horn with respect to the palatal and mid-sagittal planes, respectively.

For each species, body size was defined as the score on the first axis of a principal-components analysis of means of such species for basal length, greatest breadth, shoulder height, and body weight. Means for shoulder height and body weight of adult males were obtained from the literature (Appendix I).

To adjust for the effects of interspecific differences in body size on measures of size of horns, means of species for circumference at the base of the horn and reach of the horn were regressed against body size and the residuals were used as the scores for species in subsequent analyses. For all other measures (i.e., straightness, shape of base, percentage of the length of the horn occupied by the catching arch, and angles 1, 2, 3, and 4), the unadjusted means were used as scores for species.

Information on fighting behavior was taken from the literature. Descriptions ranged from detailed accounts of several fighting bouts to brief reports of one or a few fights. Sources for these data are given in Table 2. Each species was scored according to the occurrence of four components of fighting behavior; ramming (a charge culminating in a violent head-on collision), fencing (repeated thrust and parry, with blows primarily to the frontal surfaces of the horns), wrestling (horns are locked together and combatants attempt to push or throw their opponent off balance), and stabbing (short thrusts, with piercing blows aimed primarily at an opponent's flank or belly) and the occurrence of kneeling (versus standing) during fights. Scores ranged from 1 (observed seldomly or not at all) to 3 (observed usually or always; Table 2). Strict ramming, in which opponents charge from a distance before colliding, occurs in three of these species: Maxwell's duiker (*Cephalophus maxwelli*), African buffalo, and mountain sheep. However, in several species, fights begin with a lunge followed by a violent clashing of horns; these species were given a score of 2 for ramming behavior.

This classification is categorical rather than fully quantitative, but is sufficient to separate species into broad behavioral categories. Errors are particularly likely where descriptions of fighting are based on one or a few observations. Although the same components tend to be repeated from one fight to the next, individual

TABLE 2.—Components of fighting behavior for 21 species of bovids. Behavioral scores range from 1 (observed seldomly or not at all) to 3 (observed usually or always).

Species	Wres-					References
	Ram	Fence	tle	Stab	Kneel	
<i>Tragelaphus strepsiceros</i>	1	1	3	1	1	Kingdon, 1982; Owen-Smith, 1984; Walther, 1963
<i>Taurotragus oryx</i>	2	1	3	1	2	Kingdon, 1982; Smithers, 1983
<i>Boselaphus tragocamelus</i>	1	1	1	3	2	Sheffield et al., 1983; Walther, 1958
<i>Syncerus caffer</i>	3	1	1	1	1	Mloszewski, 1983; Sinclair, 1974, 1977
<i>Cephalophus maxwelli</i>	3	1	1	1	1	Ralls, 1975
<i>Sylvicapra grimmia</i>	1	1	1	3	3	Dunbar and Dunbar, 1979; Kingdon, 1982; Sikes, 1958
<i>Neotragus batesi</i> <sup>a</sup>	1	1	1	3	3	Kingdon, 1982
<i>Oreotragus oreotragus</i>	1	1	1	3	1	Dunbar and Dunbar, 1974; Kingdon, 1982
<i>Gazella granti</i>	1	1	3	1	1	Estes, 1967; Walther et al., 1983
<i>Gazella thomsoni</i>	2	2	1	1	1	Estes, 1967; Kingdon, 1982; Walther, 1978
<i>Litocranius walleri</i>	1	3	1	1	1	Kingdon, 1982
<i>Kobus ellipsiprymnus</i>	2	3	2	1	2	Spinage, 1982; Tomlinson, 1980; Wirtz, 1982
<i>Kobus kob</i>	2	1	3	1	1	Floody and Arnold, 1975; Kingdon, 1982
<i>Redunca arundinum</i>	2	1	3	1	1	Jungius, 1971; Smithers, 1983
<i>Hippotragus niger</i>	1	3	1	1	3	Grobler, 1974; Kingdon, 1982; Smithers, 1983
<i>Oryx gazella</i>	1	3	2	1	2	Walther, 1974, 1980
<i>Aepyceros melampus</i>	2	1	3	1	1	Jarman, 1972, 1979; Schenkel, 1966
<i>Connochaetes taurinus</i>	2	1	2	2	3	Estes, 1969; Talbot and Talbot, 1963
<i>Alcelaphus buselaphus</i>	2	1	2	2	3	Gosling, 1974
<i>Ovis canadensis</i>	3	1	1	1	1	Geist, 1971; Wells and Wells, 1961
<i>Oreamnos americanus</i>	1	1	1	3	1	Geist, 1964, 1967

<sup>a</sup> Based on observations of the suni (*Neotragus moschatus*).

fighters may lack components that usually are present in the repertoire of the species. Unfortunately, the number of fights observed usually was not reported; thus, the generality of these descriptions is unknown.

I used partial least-squares analysis to examine the overall predictability between morphology and fighting behavior. Partial least squares (Bookstein, 1982, 1986; Sampson et al., 1989; Wold, 1975) is a hybrid of regression analysis and factor analysis that is used for summarizing predictive interrelationships between two or more blocks of variables. In this application, I considered two blocks of variables, a morphological block of 10 variables (body size, straightness of horn, shape of base of horn, circumference at the base of the horn, percentage of the length of the horn occupied by the catching arch, reach of horn, and angles 1, 2, 3, and 4) and a behavioral block of five variables (ram, fence, wrestle, stab, and kneel).

Successive pairs of latent variables representing mutually independent aspects of interblock prediction were constructed from these two

blocks of variables. Each pair of latent variables consists of a linear combination of the morphological variables and a corresponding linear combination of the behavioral variables. The latent variables are constructed in an iterative fashion such that the weight for each variable within a block is proportional to the correlation between that variable and the latent variable representing the other block. Successive pairs of latent variables account for successively smaller fractions of the total predictability between morphology and behavior.

## RESULTS

Correlation coefficients between the 10 morphological variables and the five behavioral variables are given in Table 3. Seven of these are statistically significant; straightness of horn is negatively correlated with ramming ( $P < 0.01$ ), circumference at the base of the horn is positively correlated with ramming ( $P < 0.01$ ), the percentage of the length of the horn occupied by the

TABLE 3.—Correlation coefficients between measurements of morphology and measurements of fighting behavior. Morphological measurements were based on means for species. All measurements are described in the text.

	Ram	Fence	Wrestle	Stab	Kneel
Body size	0.243	0.084	0.261	-0.393	0.098
Straightness	-0.569**	0.147	0.062	0.257	0.041
Shape of base	0.007	-0.204	0.102	0.290	0.292
Circumference at the base of the horn	0.563**	-0.280	-0.369	-0.055	-0.258
Percentage of the length of the horn occupied by the catching arch	0.062	0.300	0.477*	-0.681**	-0.339
Reach	-0.295	0.489*	0.415	-0.504*	-0.158
Angle 1	-0.272	0.072	-0.117	0.275	0.499*
Angle 2	0.301	-0.032	-0.110	-0.084	0.009
Angle 3	0.242	-0.186	-0.231	0.089	0.097
Angle 4	0.377	-0.081	0.283	-0.415	-0.224

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

catching arch is positively correlated with wrestling ( $P < 0.05$ ) and negatively correlated with stabbing ( $P < 0.01$ ), reach of horn is positively correlated with fencing ( $P < 0.05$ ) and negatively correlated with stabbing ( $P < 0.05$ ), and angle 1 is positively correlated with kneeling ( $P < 0.05$ ).

The best estimate of the underlying correlation between the first pair of latent variables is 0.776 (Table 4). The statistical significance of this value cannot be tested directly (Sampson et al., 1989). However, a conservative estimate can be obtained by treating this latent-variable, correlation co-

TABLE 4.—Two-block partial least-squares analysis of morphology and fighting behavior.

	Latent variable coefficients	
	First pair	Second pair
Morphology		
Body size	-0.192	0.081
Straightness	0.095	-0.460
Shape of base	0.147	-0.024
Circumference at the base of the horn	0.016	0.596
Percentage of the length of the horn occupied by the catching arch	-0.418	0.069
Reach	-0.319	-0.390
Angle 1	0.203	-0.274
Angle 2	-0.018	0.238
Angle 3	-0.101	0.253
Angle 4	-0.243	0.271
Behavior		
Ram	-0.110	0.819
Fence	-0.221	-0.419
Wrestle	-0.353	-0.316
Stab	0.552	-0.104
Kneel	0.280	-0.203
Correlation	0.776	0.743
Percentage explained	53%	37%

efficient as though it were a correlation coefficient from a regression on two variables (F. L. Bookstein, pers. comm.), in this case  $P < 0.01$ .

This first pair of latent variables explains 53% of the total predictability between morphology and behavior. Among the morphological variables, the highest loadings are for the percentage of the length of the horn occupied by the catching arch ( $-0.418$ ) and reach of horn ( $-0.319$ ); the highest loadings among the behavioral variables are for wrestling ( $-0.353$ ) and stabbing ( $0.552$ ). These loadings indicate that the high correlation between the first pair of latent variables depends to a large extent on the association of a relatively large catching arch and long reach of horn with wrestling behavior, and a small catching arch and short reach of horn with stabbing behavior.

A plot of scores by species on the first pair of latent variables is shown in Fig. 2. At the upper right in the plot are species that employ stabbing as their primary fighting mode; the pygmy antelope (*Neotragus batesi*), common duiker (*Sylvicapra grimmia*), klipspringer (*Oreotragus oreotragus*), nilgai (*Boselaphus tragocamelus*), and mountain goat (*Oreamnos americanus*). All five have horns with a relatively short reach and little or no catching arch. Maxwell's duiker is morphologically similar to these species, but is separated from them on the behavioral axis because it differs markedly in fighting behavior, employing ramming rather than stabbing during fights.

The two alcelaphines (hartebeest and wildebeest, *Connochaetes taurinus*) have intermediate scores on both the behavioral and morphological axes. These species have horns with a moderately well-developed catching arch and a short reach; during fights they fall to their knees, clash horns, and grapple using their horns like twin rapiers to stab at the opponent's chin and throat (Estes, 1969; Gosling, 1974).

The remaining 13 species wrestle, fence, or ram. Most have horns with a relatively

well-developed catching arch and a long reach. The greater kudu (*Tragelaphus strepsiceros*), which, with Grant's gazelle (*Gazella granti*), was classified as a strict wrestler, is separated from the others by its exceptionally large catching arch and long reach of horn.

The best estimate for the underlying correlation between the second pair of latent variables is 0.743 (estimate of  $P < 0.01$ ; Table 4). This pair, which is orthogonal to the first, explains an additional 37% of the total predictability between morphology and behavior (Table 4). It reflects primarily the negative correlation between straightness of horn and ramming behavior and the positive correlation between circumference at the base of the horn and ramming behavior.

A plot of scores on the second pair of latent variables separates the African buffalo, mountain sheep, Maxwell's duiker, and wildebeest from the other 17 species (Fig. 3). African buffalo and mountain sheep have high scores on both axes, reflecting their exceptionally robust, strongly recurved horns, and strict ramming behavior. The horns of Maxwell's duiker, the only other strict rammer, are thinner (relative to body size) and considerably straighter than those of the African buffalo and mountain sheep; thus, Maxwell's duiker is distantly separated from these species on the morphological axis.

The wildebeest has a moderately high score on both axes. The wildebeest exhibits some ramming behavior, and although horns of wildebeests are not nearly as robust as those of the African buffalo or mountain sheep, they are moderately robust and are strongly recurved.

The remaining 17 species are not well-differentiated morphologically on the second pair of latent variables. Compared to the African buffalo, mountain sheep, and wildebeest, their horns are smaller in circumference (relative to body size) and straighter. The gemsbok (*Oryx gazella*) is separated from others by its especially thin,

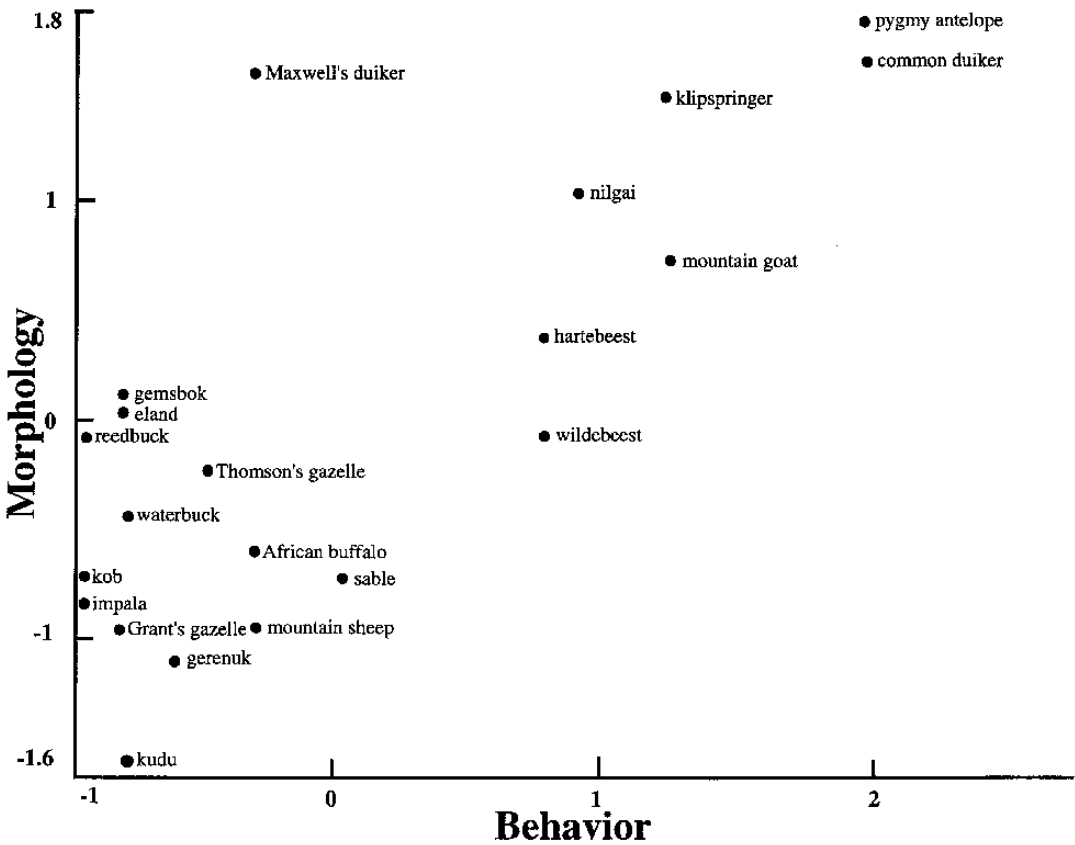


FIG. 2.—Plot of scores for species on the first pair of latent variables from a two-block partial least-squares analysis using measurements of morphology and fighting behavior for 21 species of bovids.

straight horns. With the exception of the eland, the gemsbok has the thinnest horns (relative to body size) of the 21 species examined.

DISCUSSION

Results of the partial least-squares analysis support the hypothesis that morphology of horns and fighting behavior have co-evolved. When all variables are considered simultaneously, there is a high overall correlation between morphology and behavior.

Of the 10 morphological variables, the percentage of the length of the horn occupied by the catching arch, reach of horn, circumference at the base of the horn, and straightness of horn are the greatest contributors to this relationship. The percent-

age of the length of the horn occupied by the catching arch and reach of horn together clearly separate horns used primarily in stabbing (horns with little or no catching arch and a short reach) from horns used in wrestling (horns with a well-developed catching arch and a long reach).

The percentage of the length of the horn occupied by the catching arch by itself is positively correlated with wrestling behavior ( $P < 0.05$ ) and negatively correlated with stabbing behavior ( $P < 0.01$ ). Curves of the catching arch provide a surface for holding and locking horns during wrestling matches (Geist, 1966; Walther, 1966). The largest catching arch (relative to length of horn) belongs to the greater kudu; in this species, males anchor their horns so firmly



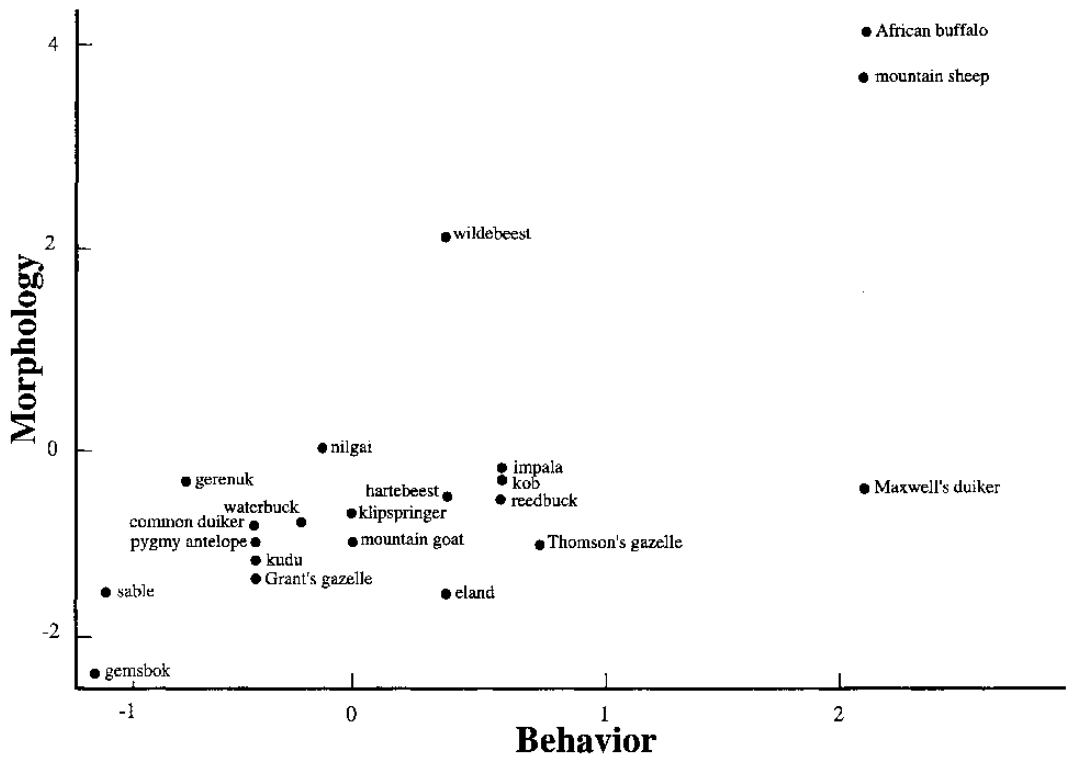


FIG. 3.—Plot of scores for species on the second pair of latent variables from a two-block partial least-squares analysis using measurements of morphology and fighting behavior for 21 species of bovids.

during fights that combatants have been found dead with the horns inextricably locked together (Walther, 1963). Reach of horn is positively correlated with fencing behavior ( $P < 0.05$ ) and negatively correlated with stabbing behavior ( $P < 0.05$ ). In species that fence, the long horns are used to deliver and parry powerful stave-like blows. Although long horns can be effective stabbing weapons, it may be difficult and dangerous to bring them into position for stabbing. Attempts to stab the body of an opponent usually do not occur in these species unless one combatant has been thrown off balance.

Fencing behavior is most highly ritualized in *Capra* (goats and ibexes), a genus that was not included in this study. The horns of *Capra* are long, robust, and scimitar shaped. In a typical fight, one or both combatants rear up onto their hind legs,

take a few steps forward, and with necks down-arched, lunge forward and downward (Alvarez, 1990; Schaffer and Reed, 1972). Blows are caught along the basal or middle one-third of the frontal surfaces of the horns. This style of fighting is associated with frontal bone sinuses (Schaffer and Reed, 1972) and well-developed neck musculature (Schaffer, 1968).

Circumference at the base of the horn and straightness of the horn separates horns used in ramming (robust, strongly recurved horns) from horns used in fencing or wrestling (relatively thinner, straighter horns). This relationship is somewhat mitigated by the inclusion of Maxwell's duiker as a strict rammer. Maxwell's duiker has horns that are considerably less robust (relative to body size) and straighter than other strict rammers examined here (African buffalo and mountain sheep). Horns of Maxwell's

duiker are directed backwards and insert well behind the orbits, originating slightly ventral to the highest point on the frontal bone. The impact from ramming in these species probably is taken, not by the horns, but by the thickened frontal bones that form the roof of the skull. Fighting has not been described in any other species of *Cephalophus*, but a thickened frontal bone, possibly associated with ramming behavior, occurs in most members of the genus (Kingdon, 1982).

My measures of the orientation of the zone of horn-stabbing (angle 1 and angle 3) and stem of horn (angle 2 and angle 4) were not significantly correlated with any particular fighting style. However, the high correlation between angle 1 and kneeling ( $P < 0.05$ ) suggests that kneeling may be advantageous to species that have horn tips that are directed posteriorly, or posteriorly and ventrally, because this arrangement facilitates the positioning of horns for stabbing (e.g., pygmy antelope), or for hooking the horns of an opponent and throwing him off balance (e.g., hartebeest).

The cross-sectional shape of the base of the horn (shape of base) is not significantly correlated with any of the measures of fighting behavior. Grant's gazelle and Thomson's gazelle (*Gazella thomsoni*) have the most strongly compressed stems of the horns, despite marked differences in their fighting behavior. This is not in accord with the hypothesis that differences in shape of the base of the horn reflect differences in the direction of forces incurred by the horns during fighting (as suggested by Kingdon, 1982).

In Fig. 4, profiles of horns from species examined in this study are superimposed on a phylogeny generated by Allard et al. (1992) using nucleotide sequences from the mitochondrial rRNA gene complex. There is general agreement that these tribes, with the possible exceptions of Bovini (Gentry, 1992) and Neotragini (Gentry, 1992; Georgiadis et al., 1990), represent monophyletic groups. However, relationships among the

tribes are not well understood. Only two clades are strongly supported by the mt-DNA data: the grouping of Tragelaphini, Boselaphini, and Bovini; the grouping of Neotragini and Antilopini (Allard et al., 1992). Nonetheless, this phylogeny serves as a useful starting point for examining the evolution of morphology of horns and fighting behavior in Bovidae.

The oldest fossil positively identified as a bovid, *Eotragus artensis* (early Miocene—Ginsburg and Heintz, 1968), had horns that were short, nearly straight, and circular in cross section (Hamilton, 1973); this construction is believed to represent the primitive condition for Bovidae (Geist, 1966). A roughly similar design of horns is retained in several extant species, including six of the 21 species examined here; nilgai, Maxwell's duiker, common duiker, mountain goat, pygmy antelope, and klipspringer. This morphology of horns is associated in all but Maxwell's duiker with a dodge-and-stab style of fighting in which males attempt to deliver piercing blows to their opponent's vulnerable flank and belly.

From this simple design, a variety of morphologies of horns have evolved. Because the measurements of the horns used in this study are continuous variables, they are not easily mapped onto the branches of the cladogram. However, it is obvious from the topology of the cladogram that convergence in morphology of horns (and associated fighting behavior) is common. For example, the most robust horns (those with the greatest circumference at the base) occur in African Buffalo and mountain sheep, the longest reach of horn, in the kudu and gemsbok, and the most-developed catching arch, in the kudu and Grant's gazelle. Of the nine measures of morphology of horns, only shape of base shows evidence of phylogenetic constraints, i.e., the most laterally compressed stems of horns are found in the three representatives of the Antilopini; gennuk (*Litocranius walleri*), Thomson's gazelle, and Grant's gazelle.

The high frequency of convergence in

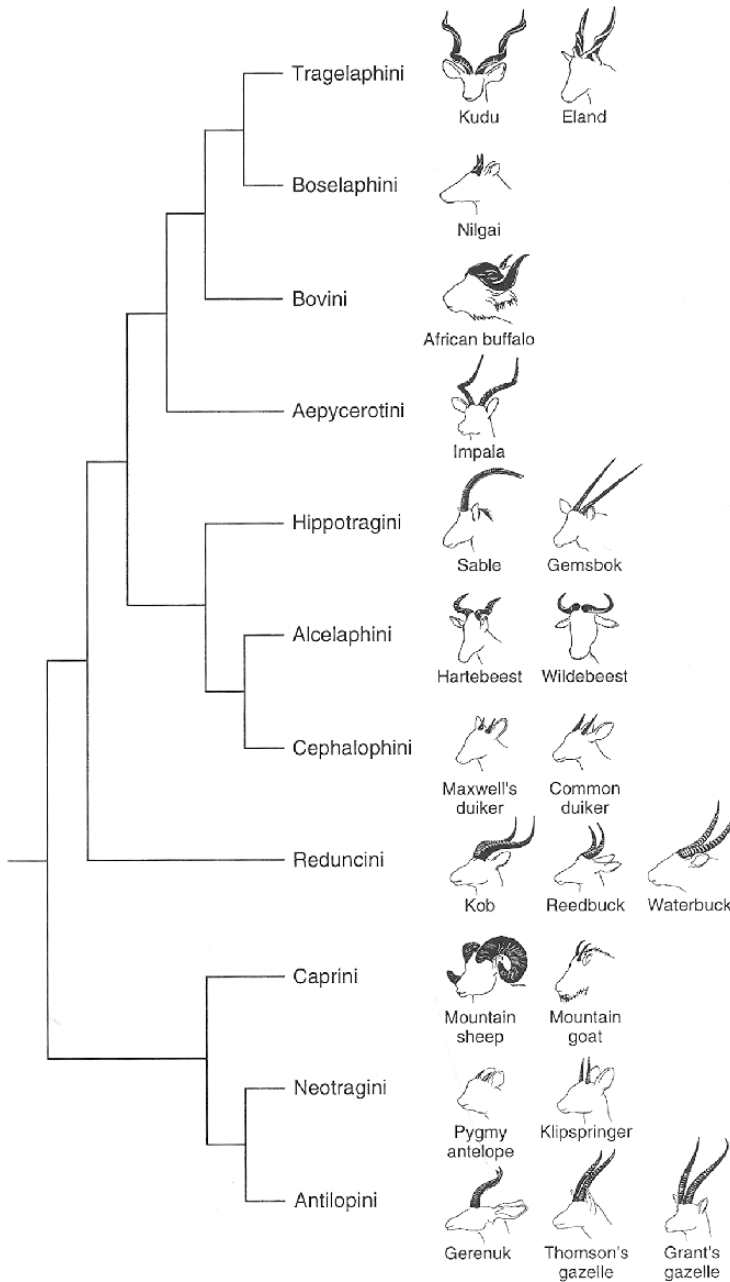


FIG. 4.—Tree of maximum parsimony (Allard et al., 1992) based on transversion substitutions in 2.7 kilobase pairs of the mitochondrial rRNA gene complex for 11 of the 12 tribes listed in Gentry, 1992; Ovibovini is excluded. Tree length is 477 and retention index is 0.43. The outgroups are sambar (*Cervus unicolor*), Chinese water deer (*Hydropotes inermis*), giraffe (*Giraffa camelopardalis*), and pronghorn (*Antilocapra americana*). Profiles of the species examined in this study have been superimposed onto the cladogram. Gentry (1992) considers the tribal affiliation of the mountain goat uncertain; it is included here with the mountain sheep (tribe Caprini) because it is a member of the same subfamily, Caprinae. Drawing by M. Van Bolt.

morphology of horns and associated fighting behavior is not surprising. Horns of bovids are sexually selected characters and, as such, are expected to show rapid evolution, resulting in a diversity of forms (West-Eberhard, 1983). Indeed, horns of bovids are so diverse that each species can be recognized by the unique shape of the horns of males. This complicates the task of characterizing patterns of variation in shape of horns across the family. The partial least-squares analysis was only moderately successful in illuminating some of these patterns. Further resolution undoubtedly could be obtained by including additional measurements and refining the measurements used in this analysis (e.g., Alvarez, 1990; Kitchener, 1988).

Because many readily observable interspecific differences in horns of bovids cannot yet be attributed convincingly to differences in fighting behavior, it is tempting to conclude that they reflect selection in other contexts or are the result of random processes. However, it is worth considering here the great variety of horns of beetles that were once thought to be non-functional and later shown, through observational studies, to have a shape that is well adapted to the species-specific fighting style (Eberhard, 1980; Otte and Stayman, 1979). Until there are more precise measurements of morphology of horns and more thorough knowledge of fighting behavior of bovids, it will not be possible to estimate the extent to which interspecific variation in morphology of horns is functionally associated with the use of horns as intraspecific weapons.

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#### APPENDIX I

Literature used as references for shoulder height and body weight: *Tragelaphus strepsiceros*, Wilson, 1965; *Taurotragus oryx*, Posselt, 1963; *Boselaphus tragocamelus*, Sheffield et al., 1983; *Syncerus caffer*, Sinclair, 1977; *Cephalophus maxwelli*, Aeschlimann, 1963; *Sylvicapra grimmia*, Wilson and Clarke, 1962; *Neotragus batesi*, Feer, 1979; *Oreotragus oreotragus*, Meinertzhagen, 1938; *Gazella granti*, Meinertzhagen, 1938; *Gazella thomsoni*, Ledger, 1963, Meinertzhagen, 1938; *Liocranius walleri*, Haltenorth and Diller, 1977, Kingdon, 1982; *Kobus ellipsiprymnus*, Spinage, 1982; *Kobus kob*, Buechner and Schloeth, 1965; *Redunca urundinum*, Haltenorth, 1963; *Hippotragus niger*, Meinertzhagen, 1938; *Oryx gazella*, Roberts, 1951, Smithers, 1983; *Aepyceros melampus*, Kingdon, 1982, Sachs, 1967; *Connochaetes taurinus*, Attwell, 1977; *Alcelaphus buselaphus*, Kingdon, 1982, Sachs, 1967; *Ovis canadensis*, Geist, 1971; *Oreamnos americanus*, Brandborg, 1955.