compared preorbital length to total skull length, and the latter is contained, in large part, within the former. Reeve and Murray (*6*) noted that reorganization was involved in horse skull evolution, but because they examined only preorbital skull length, they overlooked the fact that it was the middle portion of the skull (COM3) that elongated and displaced the tooth row anteriorly relative to the orbit and jaw joint. Reorganization of horse skull proportions occurred between 15 and 25 million years ago, with relatively little change, besides scaling effects, before and after. Unfortunately the fossil record as currently known is insufficient to shed light on the tempo of the transformation within that period.

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9. The low-crowned sample includes 13 species of the following genera: *Hyracotherium, Mesohippus, Miohippus, Kalobatippus, Hypohippus, Megahippus*, and *Parahippus*. The high-crowned sample includes 12 species of the following genera: *Merychippus, Griphippus, Pliohippus, Callippus, Cormohipparion, Hipparion, Dinohippus*, and *Equus*. Most species were represented by one or two individuals only, and most specimens are in the collections of the American Museum of Natural History.
10. For statistical comparisons without the potential bias of scaling effects, the measurements were transformed into dimensionless variables based on residuals from allometric equations. The data were transformed into logarithms (base 10) and reduced major axis equations were calculated for each variable as a function of braincase length in both groups of species (low crowned or high crowned). For each variable, a mean slope was calculated from the two group slopes and used with the total sample (combined groups) mean log x and mean log y to calculate a y intercept for a master equation for that variable. Each measurement was transformed into a dimensionless variable based on the antilog of its residual from the master equation, and the means of the transforms of each group were compared by t-tests (preceded by F-tests for differences in variances). See L. Radinsky [*Biol. J. Linn. Soc.* **15**, 369 (1981)] for discussion of this approach.
11. I thank R. Tedford for information on fossil equid systematics and V. Eisenmann, S. Emerson, and D. Bramble for critical reading of the manuscript. For permission to study fossil horses in their charge, I thank the curators of the fossil mammal collections at the American Museum of Natural History and the National Museum of Natural History. Supported by NSF grant DEB 81-00827.

22 November 1982; revised 27 May 1983

Sexual Dimorphism: The Horns of African Antelopes

Abstract. *Comparisons of the horns of males and females across genera of African antelopes indicate that male horns are better adapted for clashing or pushing against another pair of horns during intrasexual combat. The horns of females are relatively more specialized as stabbing weapons. Horns in females are found in only half the genera and in those genera where females have horns, the genera are heavier than genera with hornless females.*

In most bovid species sexual dimorphism in the size and shape of horns is striking and, in many species, the females are hornless. Because males conspicuously clash their horns during intense fights with other males, discussions of the evolution of horns have focused on males rather than females (*1–3*). Studies on the functions of horns in females are scant. Furthermore, although the disparity in horn size between males and females is believed to be the consequence of sexual selection (*4*), the extent of this disparity has not been measured nor has there been a rigorous attempt to explain the distribution across species of the presence of horns in females.

The African antelopes comprise nearly two-thirds of bovid species, and females have horns in about half of the African genera (*5, 6, 7*). Males of these species commonly use their horns in vigorous head-to-head clashes with other males (*1, 2, 8*). Aggression among females is typically less intense (*2, 9*), although serious fighting by females occasionally occurs (*10*). Individuals of both sexes are also known to use their horns in self-defense against predators (*11, 12*), and females actively defend their calves against carnivores and raptors (*11, 13*).

Because antelopes use their horns both in head-to-head combat and in stabbing conspecifics and predators, I examined two physical dimensions of horns that should relate to these uses. First was the basal area of the horn core (*14*), which reflects the maximum lateral force the horn can withstand without breaking (*15*). Lateral force will be particularly high when the horns are clashed against the horns of a conspecific. Second was the maximum reach of the horn from the top of the head (*16*), which is a measure of the distance at which another animal can be stabbed. The greater the reach of the horn, the greater the distance at which the antelope's head can be kept from an opponent or predator. The means of horn measurements (*17*) and body weights (*18*) were calculated for

Table 1. Horn breakage and relative horn thickness of adult antelopes in Lake Manyara, Ngorongoro Crater, and the Serengeti, Tanzania. Breakage was assessed with binoculars. A horn could be broken anywhere along its length, and if a horn was absent it was assumed to be broken at the base, although some missing horns may have been due to deformity, especially in female *Gazella thomsoni* (*27*). The blank spaces indicate that horns are ordinarily absent in females. The asterisk (*) indicates a significantly higher rate of broken horns than in the opposite sex in that species ($P < 0.05$). Across all genera, more males had broken horns than females ($U = 20, n_1 = 13, n_2 = 7, P < 0.05$). Relative thickness (to weight) of horns is (ln basal area) − (ln weight) (1.10), and higher values indicate thicker horns. Horn breakage is significantly related to horn thickness in males ($r_s = -0.825$, $n = 13$, $P < 0.01$), but not in females ($r_s = +0.158$, $n = 7$, not significant). Where males have relatively thin horns, breakage is highest.

Species	Males			Females		
	One or more broken horns		Thickness of horns†	One or more broken horns		Thickness of horns†
	%	*n*		%	*n*	
Synceros caffer	3.7	400*	2.59	0	258	2.01
Taurotragus oryx	6.0	50*	1.37	0	152	1.02
Tragelaphus scriptus	0	11	2.85			
Oryx gazella beisa	16.7	6	1.43	0	17	1.32
Kobus ellipsiprymnus	3.5	29	1.64			
Redunca redunca	0	25	2.73			
Damaliscus l. jimela	5.3	38	2.26	1.0	100	2.08
Alcelaphus b. cokii	3.0	33	2.73	0	100	2.11
Connochaetes taurinus	2.8	3371*	2.89	0.4	2257	2.09
Aepyceros melampus	5.6	125	2.54			
Gazella granti	0.4	287	2.74	2.8	607*	1.58
Gazella thomsoni	0.8	1000	3.03	17.3	567*	1.07
Raphicerus campestris	11.1	18	2.17			
Madoqua kirki	5.7	35	2.42			

†Relative to weight.

each genus and statistical tests are on differences across genera (*19*).

There are two principal differences in the morphology of male and female horns. First, across all genera, the horns of males and females of the same body weight are of similar reach, but the horns of males are about twice (1.96 times) as thick at the base (Fig. 1) (*20*). Second, there is dimorphism in the shape of horns in a number of genera (*Syncerus*, *Connochaetes*, *Gazella*, and *Antidorcas*), and the horns of females are less tightly curved or straighter in each case. In many of these species, the tips of the male horns point back to the base of the horn whereas the tips of the female horns always point away from the base.

The thicker and more complex shape of male horns is consistent with their use in intraspecific combat. The fact that the horns of males can theoretically withstand twice as much force as those of females makes them better adapted to withstanding the equal but opposite force experienced during a butting or pushing match with a conspecific. As would be expected if such matches involve high lateral forces, the rates of horn breakage in males are highest in species with the thinnest horns relative to body weight (Table 1). The complex horn shape in the male serves to catch the blows of an opponent's horns and to gore the opponent's neck or belly with a hooking movement of the head (*1*).

Horns of females may be thinner either as a consequence of the greater demands in females for calcium (*21*), or because their horns serve different functions. If the horns of females are thinner than those of males because of nutritional constraints yet are regularly used in a manner similar to those of males, females would be expected to break their horns more frequently than males. Instead, rates of horn breakage are consistently higher in males than in females (Table 1).

Whether or not females of a particular species have horns may depend on the following. (i) Male horns evolved independently at three to seven different times in ruminant artiodactyls at a critical body weight of about 20 kg (*3*), thus females of larger body weight may be more likely to have horns; (ii) horns may be present more often in females of open country species than forest species (*7*); (iii) females may have horns more often in gregarious species (*7*); and (iv) the presence of horns in females may relate to the degree of sexual dimorphism in body weight (*4*). In an analysis of the influence of these four variables on the presence or absence of horns in females (*22*), I found that female body weight was the principal variable affecting the presence of horns and the additional effects of other variables were not significant (*23*). Females have horns in about 75 percent of the genera with average female body weight of more than 40 kg, and females are hornless in nearly every genus where female weight is less than 25 kg.

Trends within the three lightest genera with horned females further emphasize the relation between body weight and hornlessness. *Cephalophus* includes several species of large body size (female weight > 60 kg: *C. jentinki*, *C. spadix*, and *C. sylvicultor*) and body size in this genus may be secondarily small (*3*, *24*). Whereas the horns of females are well developed in these large species, the horns of some females appear vestigial in several of the medium-sized species (10

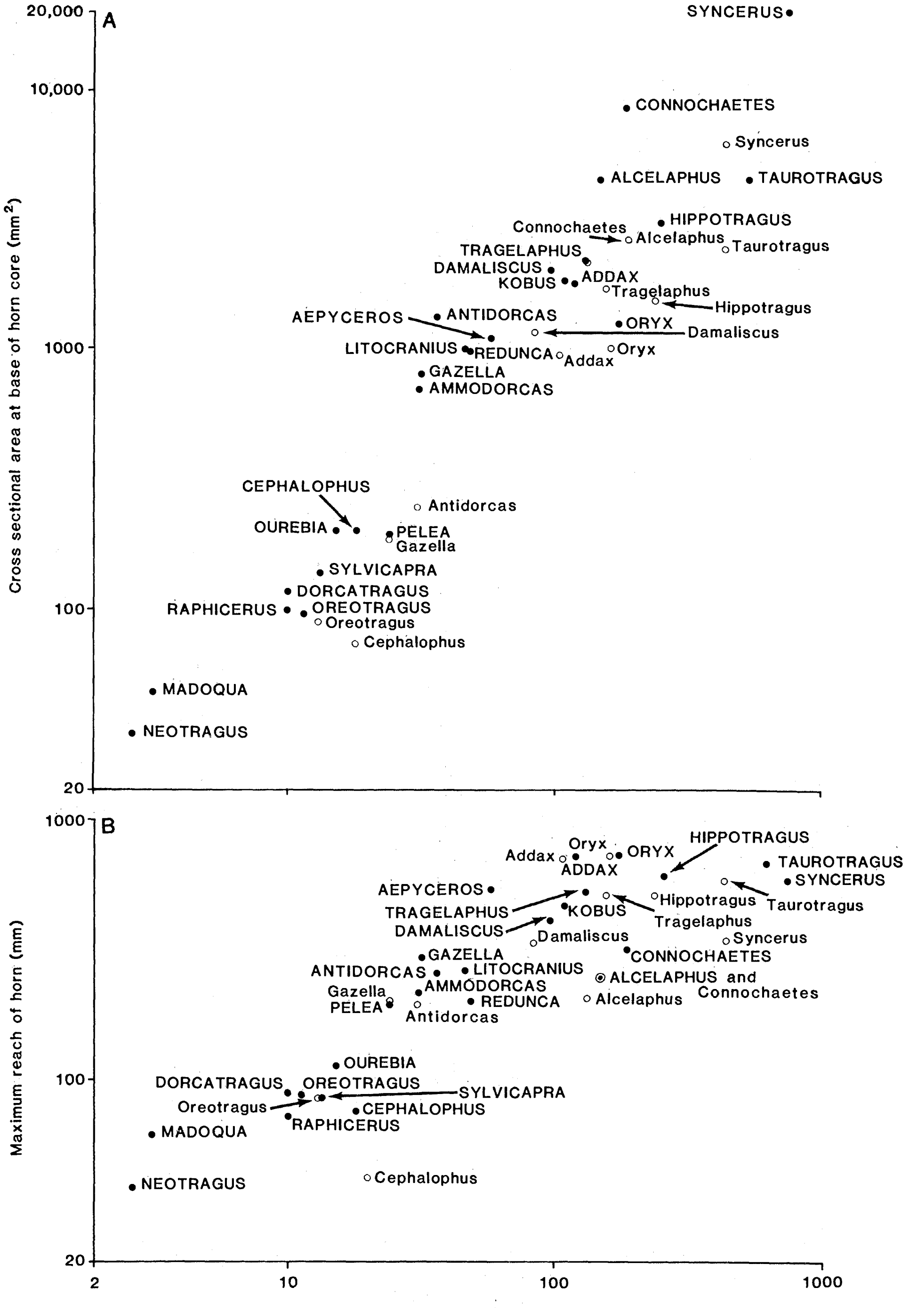

Fig. 1. Comparisons of the horns of males (●) and females (○) across all genera of African antelopes. Females are included only from those species or subspecies where females ordinarily have horns. (A) Basal area of horn core shows a similar scaling with body weight in the two sexes, but males have thicker horns for a given body weight. For males: $r^2 = 0.914$, $\ln y = (\ln x)(1.075) + 2.464$; for females: $r^2 = 0.919$, $\ln y = (\ln x)(1.127) + 1.584$. Comparison of slopes: $F = 0.152$, d.f. = 1, 34, not significant; elevations: $F = 15.732$, d.f. = 1, 35, $P < 0.001$. (B) There are no significant differences between the two sexes in the reach of horns. For males: $r^2 = 0.821$, $\ln y = (\ln x)(0.544) + 3.357$; for females: $r^2 = 0.585$, $\ln y = (\ln x)(0.559) + 3.115$. Slopes: $F = 0.010$, not significant; elevations: $F = 0.985$, not significant.

to 15 kg) (*25*) and females are often hornless in the two smallest species (< 8 kg: *C. maxwelli* and *C. monticola*) (*26*). Similarly *Gazella* contains two large species (> 40 kg) where females' horns are well developed, but in the smaller *G. thomsoni* (18.4 kg), females' horns are often vestigial (*27*). In the monospecific *Oreotragus* (12.9 kg), females have horns in only 1 of 11 subspecies (*26*).

Being straighter and thinner, the horns of females are relatively more specialized as stabbing weapons than are males' horns and as such may function more exclusively as defensive weapons against predators. The correlation between body weight and the presence of horns in females may be a consequence of the relation between body weight and antipredator behavior in antelopes: smaller species rely on crypsis or flight while large species often show direct defense against predators (*6*). Defense is more effective in larger species because the larger species are bigger than most predators and, in particular, females of large species are very much larger than predators of their young (*11, 13*). Thus, horns are most likely to be of value to females in species of larger body weight. The utility of horns as antipredator weapons has received relatively little attention, probably because of the emphasis on males in previous studies and because observations of effective defense are uncommon (*1*). While the antipredator functions of horns may only be secondary in males, effective defense has been observed by both sexes in many of the better studied species (*9, 11, 12, 13*). Horns are likely to confer a selective advantage even if they prevent predation only a few times over an average lifespan.

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17. Adult specimens of both sexes of nearly all 72 species of the 25 African genera were available either in the British Museum of Natural History, Field Museum of Natural History, National Museum of Kenya, or the Oxford University Museum. Deformed horns were excluded.
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20. Males of genera where females have horns do not differ from males of genera with hornless females either for basal area (comparison of slope: $F = 0.483$, d.f. = 1, 21, not significant; elevation: $F = 0.046$, d.f. = 1, 22, not significant) or reach (slope: $F = 2.159$, not significant; elevation: $F = 0.288$, not significant). If females are compared only to the males of their respective genera, the difference in elevation of basal area remains the only difference between males and females ($F = 9.868$, d.f. = 1, 23, $P < 0.01$).
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23. Body weights of females are from (*18*). Group size and habitat (forest, intermediate, or open) are from (*6*). Sexual dimorphism is male weight divided by female weight. Each variable was considered separately and then in a multivariate analysis with the use of the logistic regression program available from SAS [F. Harrell, in *SAS Supplemental Library User's Guide*, P. S. Reinhardt, Ed. (SAS Institute, Cary, N.C., 1980), p. 83]. Only the log of body weight and the log of group size were significantly correlated with the presence of horns when entered separately ($\chi^2 = 15.19$, $P < 0.0001$, and $= 9.85$, $P < 0.002$). Large females and those in large groups are more likely to have horns. However, weight and group size are correlated ($r = .79$, $n = 25$) (also see *6*) and when all variables are entered in a backward elimination model, body weight is the only variable significant to $P < 0.05$.
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19 February 1982; revised 31 January 1983

Corollary Discharge Provides Accurate Eye Position Information to the Oculomotor System

Abstract. *The saccadic system accurately compensates for perturbations of eye position produced by microstimulation of the superior colliculus. This requires that information about the stimulation-induced change in eye position be provided by an extraretinal source—either proprioceptive endings in extraocular muscles or a centrally generated corollary discharge. It is shown that compensation remains intact after elimination of extraocular muscle proprioception, demonstrating that corollary discharge provides accurate eye position information.*

Precise information about the position of the eyes in the orbit is required for localization of visual targets (*1*) and is an essential component of current models of the oculomotor system (*2*). The question of whether eye position signals originate from a central copy of the oculomotor command or arise peripherally from extraocular muscle proprioceptors is a fundamental issue in oculomotor physiology.

A century ago Helmholtz concluded that knowledge of eye position was derived from a "measure of the effort of will required to move the eyes" (*3*). Such an internal signal representing an intended change in eye position was referred to as corollary discharge by Sperry (*4*). Recently, physiological studies have shown that a number of brain areas contain neurons which have tonic firing rates correlated with eye position (*5*). These neuronal populations are functionally close to the final oculomotor output and project to other centers involved in the control of eye movements. Such physiological and anatomical properties suggest that these neurons generate a corollary discharge which could be used to represent eye position. Unlike most