are not clear. Abboud *et al.* (*15*) reported that smoking two to four cigarettes produced a limited α_1-PI-inactivating effect.

We have investigated two differences in experimental design between our study and the previous studies but could not account for the differences in findings. First, the smoking group in the study by Gadek *et al.* (*7*) and by Carp *et al.* (*8*) had a more extensive smoking history (27 ± 7 and 18 ± 1 pack years, respectively, compared with 8 ± 1 for our smoking group). However, we found no significant difference in the mean functional α_1-PI as a percentage of protein calculated for the six heaviest smokers in our study (1.5 to 2 packs per day for 9 ± 2 years) as compared with our entire smoking group (2.9 ± 0.1 versus 2.7 ± 0.1 percent, respectively, for ^{3}H-PPE–specific α_1-PI). The addition of sodium azide, a bactericidal agent, to the BAL fluid samples did not account for the difference in findings. Before the addition of azide, we found peroxidase-like activity, with *o*-dianisidine used as substrate, in concentrated BAL fluid samples from smokers and less activity in samples from nonsmokers. This activity was suggestive of neutrophil-derived myeloperoxidase, which can readily inactivate α_1-PI in the presence of H_2O_2 and a halide but is inhibited by sodium azide (*4*). However, Nauseef, using a sensitive procedure developed in his laboratory (*16*), did not detect immunoreactive myeloperoxidase in portions of BAL fluid representing 6 percent of the samples from two smokers. Furthermore, incubation of portions of BAL samples for several weeks at 4°C in the absence of sodium azide failed to depress the level of functional α_1-PI in comparison with portions of the same samples to which sodium azide had been added.

Although the peroxides in smoke from different cigarettes are thought to variably reduce the elastase inhibitory capacity of α_1-PI (*17*), we did not investigate the effect of cigarette brand or the presence of filters on levels of functional α_1-PI in the BAL fluid of smokers. Also, our study does not exclude the possibility of a very rapid recovery of functional α_1-PI in the lungs after cigarette smoke–induced oxidation or of a significant smoke-induced depression of functional α_1-PI restricted to small localized portions of the lower respiratory tract.

Even though the lower respiratory tracts of smokers and nonsmokers may contain comparable levels of antielastase activity, smokers presumably are still at greater risk of developing emphysema because of an imbalance in the elastase-antielastase system. The sedimented BAL cells from our smoking group contained, on average, more than five times as many neutrophils and alveolar macrophages as we found in nonsmokers. If cells obtained by lavage are representative of the numbers of cells within the lungs, the elastase burden of smokers is clearly increased. Our results suggest that additional studies of the effects of cigarette smoke on α_1-PI in the lower respiratory tract are needed and that antioxidants might not offer protection against the development of emphysema in smokers.

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Allometry and Reorganization in Horse Skull Proportions

Abstract. *Allometric analysis of skull proportions in 25 species of fossil equids indicates that both scaling effects (allometry) and reorganization were factors in the evolutionary transformation of horse skulls. A relatively longer preorbital portion of the skull resulted from the ventral and forward displacement of the tooth row relative to the jaw joint and the orbit when high-crowned teeth evolved. Correlated with the increased distance between jaw joint and tooth row is an increase in the relative size of the attachment areas of masseter and internal pterygoid muscles.*

Horses have one of the longest and richest fossil records of any group of mammals. Their record extends back 55 million years and documents major morphological changes in feeding and locomotor systems. For these reasons, the fossil record of horses has been an important source of textbook samples of evolutionary phenomena (*1*). Most work on fossil horses has dealt with details of dental anatomy (*2*). There have been a few major studies of the evolution of the limbs (*3*) and of differences in skull morphology among closely related species or genera (*4*).

Our knowledge of the evolutionary transformation of horse skulls has for the past 40 years rested primarily on two studies, which came to contradictory conclusions. Robb (*5*), who analyzed changes in skull proportions in horse evolution by comparing preorbital length to total skull length in 13 species of fossil horses, concluded that the relatively long muzzles of modern horses resulted entirely from allometry—size-related changes in proportions that occurred during evolution from small ancestral horses to the large modern ones. Seven years later, Reeve and Murray (*6*) reanalyzed Robb's data. They compared preorbital length to braincase length (that is, skull length minus preorbital length) and concluded that there had been a reorganization of skull proportions to accommodate an enlarged battery of grinding teeth that evolved about 15 million years ago. From an analysis of measurements of juvenile modern horses, Reeve and Murray concluded that the reorganization in skull proportions involved an increase in the size of the facial rudiment at an early stage of growth. Later workers followed either Robb, and stated that scaling effects account for modern horse skull proportions (*7*), or Reeve and Murray, and concluded that horse skull proportions were reorganized by an increase in size of the facial portion of the skull (*8*).

In the almost 50 years that have elapsed since Robb collected his data, a large amount of new fossil horse material has become available for study. My work is based on measurements taken on representatives of 25 species of fossil horses, ranging from *Hyracotherium*, the oldest horse (betwen 50 to 55 million years old), to *Equus*, the sole surviving genus of equid. The fossil horse species were divided into two groups, depending on whether they have low-crowned (height less than length) or high-crowned cheek teeth (*9*). Measurements were selected to reflect functionally significant aspects of cranial morphology and features that had been perceived by earlier workers as having changed significantly in proportions in horse skull evolution (Fig. 1). Measurements were compared with braincase length for a standard of comparison and were analyzed for scaling effects and differences between species with low-crowned or high-crowned cheek teeth (*10*).

The results (Table 1) suggest that changes in skull proportions during the evolution of horses resulted in part from allometric (scaling) effects, and in part from reorganization, but not the reorganization that had been suggested. Allometry is indicated by the scaling exponent of the facial portion of the skull—measured from the back of the last molar (TRL in Fig. 1). It scales with an exponent of 1.24, indicating that horses with longer braincases will have disproportionately longer facial portions of the skull. However, there is no difference in TRL proportions between species with low-crowned or high-crowned teeth (see TRL transform means in Table 1).

Table 1. Reduced major axis statistics (*10*) for fossil horses with low-crowned teeth (above) and high-crowned teeth (below). Slopes are given ± standard errors. All measurements are compared to braincase length. See Fig. 1 for abbreviations and measurements.

Variable	Slope	r	Mean slope	Log y intercept	Mean of transforms
TRL	1.257 ± 0.061	0.985	1.236	0.205	0.988
	1.215 ± 0.040	0.994			1.015
COM3	1.206 ± 0.091	0.965	1.244	−0.135	0.879*
	1.282 ± 0.101	0.969			1.177
COM1	1.220 ± 0.074	0.977	1.228	0.087	0.936*
	1.236 ± 0.092	0.969			1.082
MAM	1.387 ± 0.113	0.959	1.311	−0.050	0.903*
	1.236 ± 0.087	0.972			1.131
SMSL	1.142 ± 0.080	0.967	1.283	−0.019	0.929*
	1.425 ± 0.065	0.987			1.092

*Difference significant at the 0.01 level.

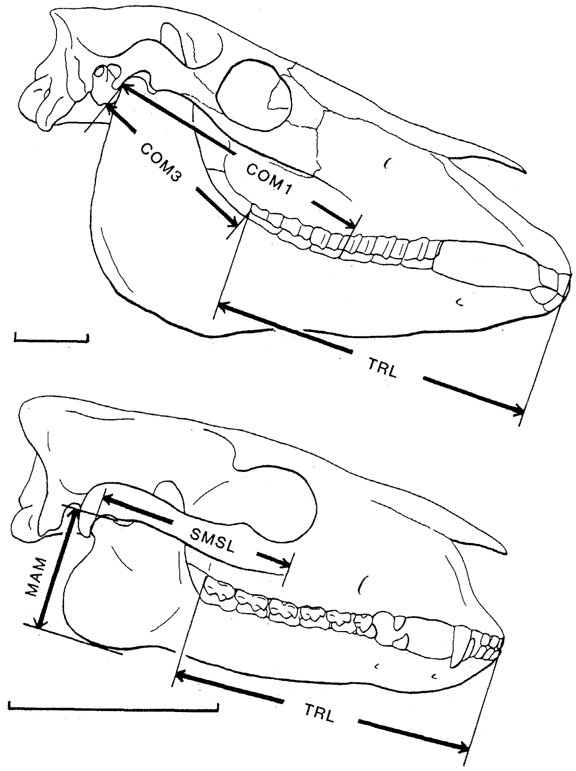

Fig. 1. Skulls of *Equus caballus*, domestic horse (top), and *Hyracotherium vassaciense*, a 50-million year old equid (bottom), with measurements indicated. COM1, condyle to front of first lower molar; COM3, condyle to back of lower third molar; MAM, condyle to ventral border of mandible; SMSL, postglenoid process to anterior edge of malar ridge (superficial masseter scar); TRL, from back of last upper molar to front of premaxilla. All measurements were compared to braincase length, measured along the ventral midline from the foramen magnum to the level of the orbital foramen. Scale bars, 5 cm.

A major reorganizational change occurred, but not from an increase in the length of the tooth-bearing portion of the skull. Rather, there was a ventral and forward displacement of the tooth row relative to the jaw joint and the orbit. The distance from the jaw joint to the tooth row (COM3 in Fig. 1) is an average of 34 percent greater (relative to braincase length), and the distance from the jaw joint to the ventral border of the mandible (MAM in Fig. 1) is an average of 25 percent greater in the high-crowned species (transform means in Table 1). As a result of these changes, the anterior border of the orbit lies above the last molar in *Equus*, whereas it is in its primitive position above the first molar in *Hyracotherium* (Fig. 1). The dental battery and eyeball are relatively large in young individuals, and these changes in skull proportions, which shift the cheek teeth anterior to the orbit, may have resulted from the need for space to accommodate high-crowned teeth within the maxilla in early ontogenetic stages.

The distance between the jaw joint and the middle of the cheek tooth row (COM1 in Fig. 1) is an average of 16 percent greater in the high-crowned species (Table 1), suggesting a relatively greater resistance arm, or outlever, in the jaw apparatus. Correlated with this increase in resistance arm is an apparent increase in size and lever arm (distance to jaw joint) of two important jaw muscles, the masseter and internal pterygoid, as indicated by the relatively larger MAM and SMSL in the high-crowned horses (Table 1 and Fig. 1). This suggests increased power or efficiency of these muscles, perhaps in response to the need to maintain comparable pressure at the occlusal surface of more forwardly located (relative to the jaw joint) cheek teeth.

These findings indicate that the earlier analyses of horse skull evolution were only partly correct. Robb (*5*) noted that scaling effects were involved but missed reorganizational changes because he 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.
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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.