Unbranched horns

Bovid Horns

Figure 1. Dama gazelle horns are ridged and "S" shaped, curving first backwards and then upward. Horns are present in both sexes but tend to be larger and thicker in males, ranging from 20-43 cm long (1). This gazelle's choice in headwear complements his horns nicely. Photo courtesy of the San Diego Zoo.

Figure 2. Sitatungas sport ridged, spiraled horns that twist 1-1.5 times, reaching up to 90 cm long. Horns are only present in males (2). Photo courtesy of the African Wildlife Foundation.

Figure 3. The Scimitar-horned oryx has smoother, thinner and more fragile horns than the Sitatunga or Dama gazelle. Both males and females grow horns that curve up and over the back, reaching 100-125 cm (3). Photo courtesy of the Smithsonian National Zoo.
Phenotypic Evolution

Headgear (referring to horns, antlers, ossicones, and prongs) arose far before the differentiation of the family Bovidae from other ruminant families. According to the most recent molecular data, a strong case can be made for a single origin of headgear, arising after the split from the headgear-less family Tragulidae (Figure 5). The earliest moschid fossils show an ancestral lack of headgear similar to Tragulidae, while the earliest fossils from all other families show the presence of headgear; initial phylogeny attempts placed Moschidae close to Tragulidae with some uncertainty. Arguments based only on evidence from the fossil record can be made for multiple origins of headgear in the ruminant families. However, modern molecular phylogenies nestle Moschidae with Bovidae. Arguments based purely on molecular data hypothesize a single origin of headgear followed by a reversal in Moschidae (4). There is still debate over how to consolidate these two conflicting views into a single, most parsimonious phylogeny.

All species falling under the family Bovidae have unbranched horns. The most widely accepted hypothesis explaining the original purpose of horns is that they arose as weapons for combat, both against predators and against conspecifics (5). The utility of horns as defense against a large predator is obvious, but the problem with this hypothesis lies in the great diversity of horn size and shape seen amongst bovids. If horns arose as a means of predator defense, we would expect to see "one good pair of horns", most likely short and sharp, that would function as an efficient way to injure a predator (6). This single effective horn type would be conserved across species. Why, then, do we see so such a vast array of horn designs today? One possible explanation is that different horn shapes are effective against different predators, but this logic falls apart when we consider that bovids sharing habitats can exhibit dramatically different horn morphology. For example, picture a rocky mountain goat and a big horn sheep; the goat's horns weigh between 100 and 120 grams, while the sheep's horns weigh about 6,900 grams, yet the two animals can often be found together in the same habitat (5).

These differences can begin to be explained when we delve further into conspecific competition. While horns may have originally functioned as puncturing weapons, the cost of such a battle between two conspecifics would be quite high. A logical defense against an attack from a horned conspecific would be to use one's own horns to deflect the blow; selection would begin to favor horns that adequately minimized damage from other horns. Over time selection pressure would shape the horns such that injury during dominance fights is minimized. The twisted and ridged horns of the Sitatunga and Dama gazelle, while not very effective for inflicting damage, are very effective for locking two individuals together while they push and shove during a fight (Figures 1 and 2). This fighting strategy also would promote selection for larger horns that would deter a smaller competitor from fighting in the first place, conserving resources and avoiding injury. Displays of body and horn size prior to fighting are common behaviors in bovids, supporting the idea that the current function of horns is more about threatening than injuring (5). Because they minimize injury while still establishing dominance, twisted, ridged horns are adaptive in the context of display and wrestling behavior. Additionally, female Dama gazelles possess smaller horns than males, and female Sitatungas lack horns altogether; sexual selection driven by male-male competition correlates with larger horns in males and smaller horns in females. Because of the twisted shape and sexual dimorphism present in Dama gazelle and Sitatunga horns, the most supported hypothesis for horn evolution is a progression from selection for predator defense to sexual selection for displays of dominance (Figure 5).

In the Scimitar-horned oryx, whose horns are smoother, more slender, and more fragile, sexual selection for display seems to have outpaced selection for true fighting horns. Male Scimitar-horned oryxes do participate in the same ritualistic displays and dominance battles seen in other bovids, but their horns are prone to breakage. The oryx's long horns seem to be more functional as intimidation factors than as actual fighting elements. Interestingly, long horns are found in both male and female oryxes. One hypothesis for the existence of horns in female bovids maintains that horns on a mother may act as a deterrent against aggression toward her male offspring (7). Female horns and other secondary sexual characteristics may be adaptive by increasing the survival of a mother's sons.

Sexual selection is the driving factor behind differences across species as well as between genders of modern bovid horn shapes. Sexual selection can be a strong force that influences numerous physical characteristics and behaviors besides horn morphology; a notable example in most species, including our three focal species, is body size.
Development and Gene Regulation

While little is known about the mechanisms of development or gene regulation of bovid horns, current research is actively demystifying some of the processes that occur. Bovid horns are hypothesized to develop from bony horn-like outgrowths on the head, as well as from the skin covering these outgrowths. The horns grow independently of the skull bones, extending from the skin covering the forehead, but fuse with the skull shortly after birth (5). First, a precursor called the horn anlage forms from the connective tissue at the future horn site. The next stage involves the formation of a structure called the *os cornu*, a nodule in the same tissue, but it is still unclear how the *os cornu* forms. It may form from the horn anlage, or may develop from the dermis or cartilage; sometimes it may not develop at all. The developing horn next attaches itself to the skull bone, continuing to grow at the surface. This structure becomes the core of the horn and grows rapidly early in life but more slowly with aging, although it will continue to undergo remodeling throughout an individual's entire lifespan (4). The porous horn core is a relatively conserved homologous structure among bovids (5). The *Polled* locus has been implicated in male horn formation in cattle, which belong to the bovid subfamily Bovinae. Mutations in the *Polled* locus have been shown to interfere with horn ontogenesis (8). It is possible that mutations in the *Polled* locus, or a homolog of the locus, are responsible for the reversion of headgear we saw in the family Moschidae (Figure 4). Testosterone has also...
been shown to play a role in male horn formation, and rates of horn growth have been linked to sex hormone cycles (4). Larger horn sizes found in males of many bovid species may be associated with the presence of testosterone and other male-specific hormones, but details about the pathways or relationships between hormones and horn growth are still not well understood.

The outer keratin sheath of the horn is the structure we see when we observe the great diversity of horn shapes and sizes among bovids. Unlike the antlers of cervids, the horn sheath is never shed (5). Layers of keratin are grown outward from skin on the horn core, with the oldest keratin at the tip of the horn. Variety in horn shapes and sizes is attributed to differential production of keratin at the horn's base (4). Modulation of keratin production zones would allow the creation of detailed horn morphology plans. The family of genes responsible for keratin production (labeled KRT genes) are found in many organisms, ranging from humans to bovids to mice. At least 54 KRT genes have been identified in humans. Because the keratin sheath grows from the skin around the horn core, bovid homologs of specific KRT genes that are expressed in the human epidermis likely play a large role in horn growth. These include KRT1, KRT5, KRT10, and KRT14 (9). In humans, keratin genes are regulated by a complicated and vast array of transcription factors and regulatory sites. Such a dense network of interactions allows for specific and precise alterations of keratin expression in various tissues. Transcriptional regulation of sites in the promoter regions of KRT genes is the most important regulatory mechanism. Specifically, the transcription factors Sp1, AP1 and AP2 have been shown to regulate many keratin genes in humans (10). An analogous system likely exists in bovids, where small changes in the intensity or timing of expression of KRT genes would create different horn sizes, while modulation of expression across regions of tissue could produce ridges and twists.

References