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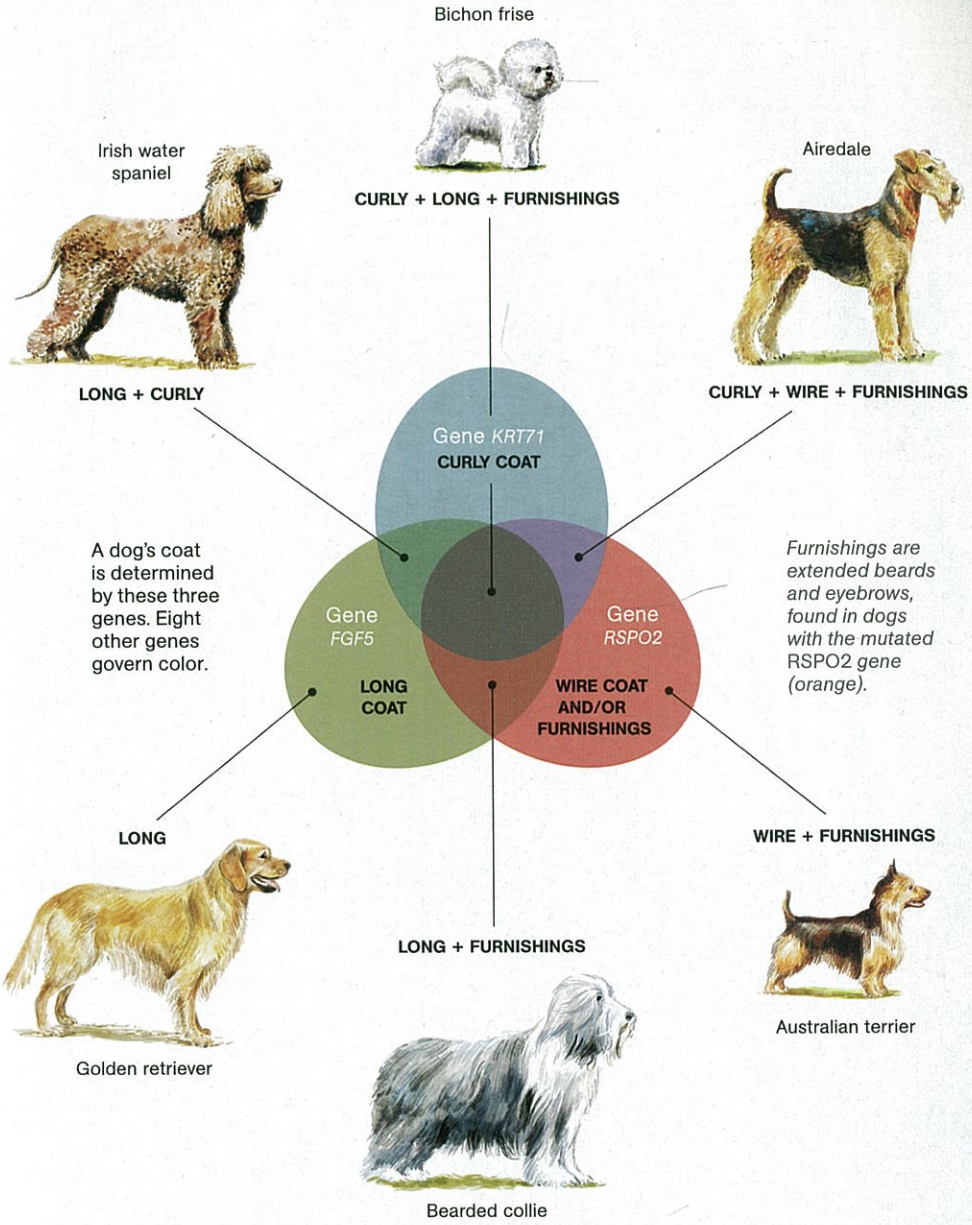
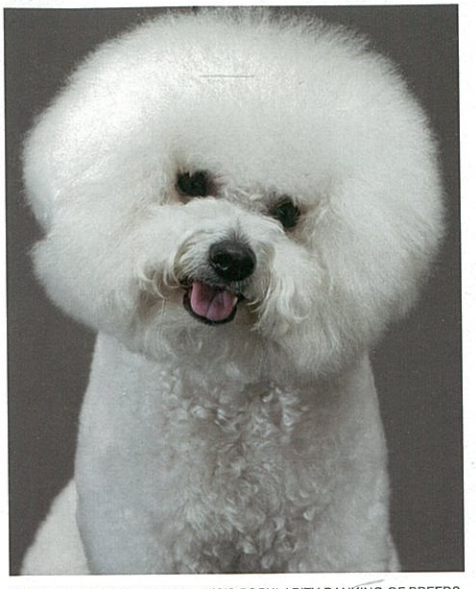



**HAIR OF THE DOG** Hundreds of genes interact to produce a physical trait in humans and most mammals. For dog traits, the magic number is usually three or fewer. The type of coat a dog wears depends on the three genes shown above. Mutations in these genes create a coat that's long, curly, wiry, or a combination. If none of the three genes are mutated, the dog will have the short, smooth coat of breeds like beagles and basset hounds—and the dog's ancestor, the gray wolf.

JOHN TOMANIO, NGM STAFF. DOG ILLUSTRATIONS: DAN WILLIAMS
SOURCE: ADAM BOYKO, CORNELL UNIVERSITY

BY EVAN RATLIFF · PHOTOGRAPHS BY ROBERT CLARK



BICHON FRISE, 37TH ON THE AKC'S POPULARITY RANKING OF BREEDS

**It's an unusually balmy mid-February afternoon in New York City, but the lobby of the Hotel Pennsylvania is teeming with fur coats.**

The wearers are attendees of what is undoubtedly the world's elite canine mixer, one that takes place each year on the eve of the Westminster Kennel Club dog show. Tomorrow the nation's top dogs from 173 breeds will compete for glory across the street at Madison Square Garden. But today is more akin to a four-legged meet-and-greet, as owners shuffle through the check-in line at the competition's official lodgings. A basset hound aims a droopy eye across a luggage cart at a wired-up terrier. A pair of muscled Rhodesian ridgebacks, with matching leather leashes, pause for a brief hello with a fluffy Pyrenean shepherd. Outside the gift shop a Tibetan mastiff with paws the size of human hands goes nose to nose with a snuffling pug.

The variety on display in the hotel lobby—a dizzying array of body sizes, ear shapes, nose lengths, and barking habits—is what makes dog lovers such obstinate partisans. For reasons both practical and whimsical, man's best friend has been artificially evolved into the most diverse animal on the planet—a staggering achievement, given that most of the 350 to 400 dog breeds in existence have been around for only a couple hundred years. The breeders fast-forwarded the normal pace of evolution by combining traits from disparate dogs and accentuating them by breeding those offspring with the largest hints of the desired attributes. To create a dog well suited for cornering badgers, for instance, it is thought that German hunters in the 18th and 19th centuries brought together some combination of hounds—the basset, a native of France, being the likely suspect—and terriers, producing a new variation on the theme of dog with stubby legs and a rounded body that enabled it to chase its prey into the mouth of a burrow: hence the dachshund, or "badger dog" in German. (A rival, flimsier history of the breed has

*Evan Ratliff wrote on the origins of domestication in the March 2011 issue. Brooklyn-based Robert Clark's last dog, a pit bull named Leo, now lives on a farm.*

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**FAMILY TIES** Analyzing the DNA of 85 dog breeds, scientists found that genetic similarities clustered them into four broad categories. The groupings reveal how breeders have recombined ancestral stock to create new breeds; a few still carry many wolflike genes. Researchers named the groups for a distinguishing trait in the breeds dominating the clusters, though not every dog necessarily shows that trait.

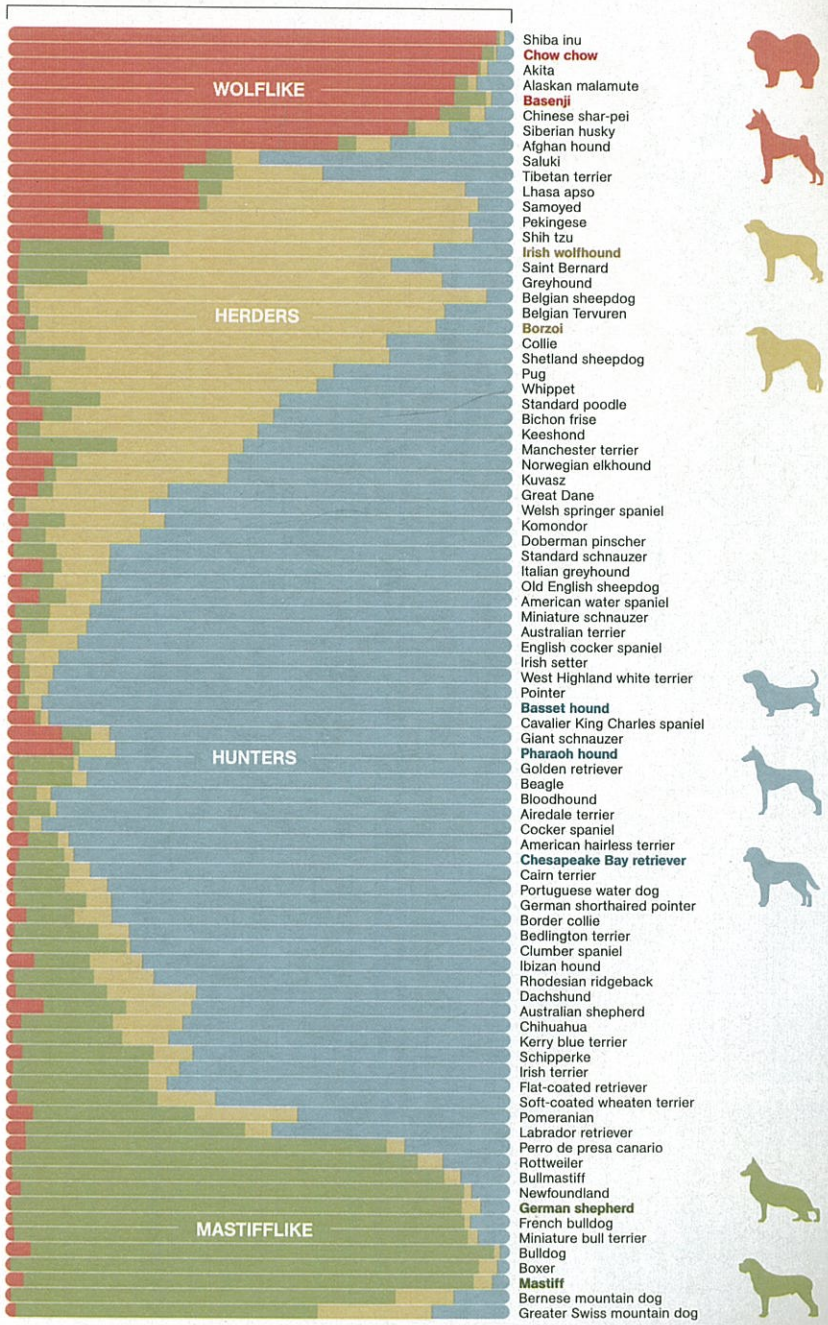
The length of the colored bars in a breed's genetic profile shows how much of the dog's DNA falls into each category.

**WOLFLIKE**
With roots in Asia, Africa, and the Middle East, these breeds are genetically closest to wolves, suggesting they are the oldest domesticated breeds.

**HERDERS**
Familiar herding breeds such as the Shetland sheepdog are joined by breeds never known for herding: the greyhound, pug, and borzoi. This suggests those breeds either were used in the creation of classic herding dogs or descended from them.

**HUNTERS**
Most in this group were developed in recent centuries as hunting dogs. While the pharaoh hound and Ibizan hound are said to descend from dogs seen on ancient Egyptian tombs, their placement here suggests they are re-creations bred to resemble ancient breeds.

**MASTIFFLIKE**
The German shepherd's appearance in this cluster, anchored by the mastiff, bulldog, and boxer, likely reflects its breeding as a military and police dog.




JOHN TOMANIO, LAWSON PARKER, NGM STAFF
SOURCE: HEIDI G. PARKER, NATIONAL HUMAN GENOME RESEARCH INSTITUTE, NATIONAL INSTITUTES OF HEALTH

LIKE ITS ANCESTOR THE GRAY WOLF, THE BASENJI, ONE OF THE MOST ANCIENT BREEDS, DOESN'T BARK.

it dating back, in some form, to ancient Egypt.) Pliable skin served as a defense mechanism, allowing the dog to endure sharp-toothed bites without significant damage. A long and sturdy tail helped hunters to retrieve it from an animal's lair, badger in its mouth.

The breeders gave no thought, of course, to the fact that while coaxing such weird new dogs into existence, they were also tinkering with the genes that determine canine anatomy in the first place. Scientists since have assumed that underneath the morphological diversity of dogs lay an equivalent amount of genetic diversity. A recent explosion in canine genomic research, however, has led to a surprising, and opposite, conclusion: The vast mosaic of dog shapes, colors, and sizes is decided largely by changes in a mere handful of gene regions. The difference between the dachshund's diminutive body and the Rottweiler's massive one hangs on the sequence of a single gene. The disparity between the dachshund's stumpy legs—known officially as disproportionate dwarfism, or chondrodysplasia—and a greyhound's sleek ones is determined by another one.

The same holds true across every breed and almost every physical trait. In a project called CanMap, a collaboration among Cornell University, UCLA, and the National Institutes of Health, researchers gathered DNA from more than 900 dogs representing 80 breeds, as well as from wild canids such as gray wolves and coyotes. They found that body size, hair length, fur type, nose shape, ear positioning, coat color, and the other traits that together define a breed's appearance are controlled by somewhere in the neighborhood of 50 genetic switches. The difference between floppy and erect ears is determined by a single gene region in canine chromosome 10, or CFA10. The wrinkled skin of a Chinese shar-pei traces to another region, called HAS2. The patch of ridged fur on Rhodesian ridgebacks? That's from a change in CFA18. Flip a few switches, and your dachshund becomes a Doberman, at least in appearance. Flip again, and your Doberman is a Dalmatian.

"The story that is emerging," says Robert Wayne, a biologist at UCLA, "is that the diversity in domestic dogs derives from a small genetic tool kit."

Media reports about *the* gene for red hair, alcoholism, or breast cancer give the false impression that most traits are governed by just one or a few genes. In fact, the Tinkertoy genetics of dog morphology is a complete aberration. In nature, a physical trait or disease state is usually the product of a complex interaction of many genes, each one making a fractional contribution. Height in humans, for instance, is determined by the interaction of some 200 gene regions.

So why are dogs so different? The answer, the researchers say, lies in their unusual evolutionary history. Canines were the earliest domesticated animal, a process that started somewhere between 20,000 and 15,000 years ago, most likely when gray wolves began scavenging around human settlements. Dog experts differ on how active a role humans played in the next step, but eventually the relationship became a mutual one, as we began employing dogs for hunting, guarding, and companionship. Sheltered from the survival-of-the-fittest wilderness, those

semidomesticated dogs thrived even though they harbored deleterious genetic mutations—stumpy legs, for instance—that would have been weeded out in smaller wild populations.

Thousands of years later, breeders would seize on that diverse raw material when they began creating modern breeds. They tended to grab traits they desired from across multiple breeds—or tried to rapidly replicate mutations in the same one—in order to get the dog they wanted. They also favored novelty, since the more distinct a line of dogs appeared, the more likely it was to garner official recognition as a new breed. Such artificial selection tended to favor single genes with a large impact, allowing traits to be fixed more rapidly than groups of smaller-impact genes ever could.

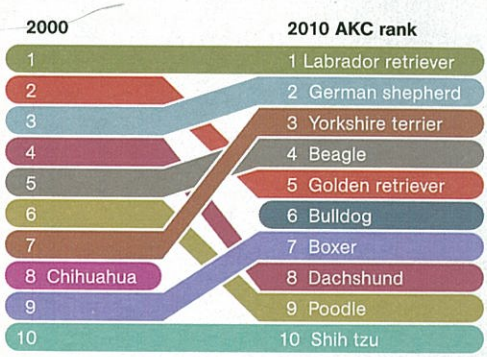
"It's kind of like when you set your remote control to control your TV, your stereo, and your cable," says Carlos Bustamante, a CanMap geneticist now at Stanford University. "You hit the on-off switch, and it does them all."

This revelation has implications the scientists are just beginning to unravel—most important, for the understanding of genetic disorders in humans. Already, more than a hundred dog diseases have been mapped to mutations in particular genes, many of them with human counterparts. Those diseases may have a whole array of mutations leading to a risk of disease in dogs, as they do in us. But because dogs have been genetically segregated into breeds developed from just a few original individuals, each breed has a much smaller set of errant genes—often only one or two—underlying the disease. For instance, Cornell researchers studying the degenerative eye disease retinitis pigmentosa—shared by humans and dogs—found 20 different canine genes causing the disorder. But a different gene was the culprit in schnauzers than in poodles, giving researchers some specific leads for where to start looking in humans. Meanwhile a recent study of a rare type of epilepsy in dachshunds found what appears to be a unique genetic signature, which could shed new light on the disorder in us as well.

In short, while the Victorian breeders were crafting dogs to suit their tastes, they were also creating genetically isolated populations, little knowing how useful they might be to scientists in the future. The possibilities are especially abundant for cancer, certain types of which can show up as often as 60 percent of the time in some dog breeds but only once in every 10,000 humans.

"We are the people who are doing the genetics," says Elaine Ostrander, who studies dog evolution and disease at the National Human Genome Research Institute at NIH. "But breeders are the people who have done all the fieldwork."

One category of trait that has so far proved resistant to the CanMap analysis is behavior. Only a single mutant behavioral gene has been identified to date: the dog version of the gene for obsessive-compulsive disorder in humans, which can cause Doberman pinschers to obsessively suck on their fur to the point of bleeding. More common characteristics such as loyalty, tenaciousness, or the instinct to herd clearly have genetic underpinnings. But they can also be affected by factors ranging from a dog's nutrition to the presence of children in the house, making them difficult to quantify rigorously enough to study. Nevertheless, "we've probably got as good a shot, if not better, of understanding behavior in dogs over other animals," says Stanford's Bustamante. After all, he points out, there are millions of dog lovers out there willing and eager to help with the fieldwork. ▯




**TOP DOGS** The most popular breeds in 2000 and 2010 by American Kennel Club registrations

NGM ART
SOURCE: AMERICAN KENNEL CLUB

Oakley, a pug (foreground), and Little Dude, a Saint Bernard, stand witness to the immense morphological diversity of their species. If humans varied as much in height, the smallest would be two feet tall and the tallest would measure some 31 feet.

**Dog breeds were created by human beings. The village dog created itself.**

# THE FOREVER DOG

**By Evan Ratliff**

LABRADORS MAY BE the most popular breed of dog, but the most populous kind is no breed at all. That distinction goes to the humble village dog scratching out a semiwild living in and around human settlements.

While a postdoc at Cornell University a few years ago, Adam Boyko became curious about the little-studied village vagrants. Though dogs were first domesticated 20,000 to 15,000 years ago, most breeds go back only a few hundred years. Perhaps village dog DNA might shed light on the long, early history of domestication, when canines were hanging around humans yet not under our domain. But how to get samples?

As it happened, around the same time Boyko's brother Ryan had married, and he and wife Corin were looking for a cheap honeymoon off the beaten track. The three Boykos decided to merge their two quests. Adam—now at Cornell's College of Veterinary Medicine—obtained a grant, then enlisted Ryan and Corin to spend their honeymoon traveling around Egypt, Uganda, and Namibia, befriending villagers and local vets. They collected DNA from more than 300 village dogs.

When the samples were analyzed, most of the village dogs turned out to be as closely related to wolves as they were to fully domesticated dogs. Rather than being mixed-breed mutts that had gone feral in historical times, the village dogs had been eking out an existence on the human fringe for millennia. Their genomes thus reflected a state of early domestication, before artificial selection and inbreeding directed by humans had taken over. "When you are looking at village dogs," Adam Boyko says, "you have something more akin to natural selection, albeit in an environment that's managed by humans."

Unexpectedly, the study also helped to challenge the reigning view on the place where dogs first appeared. Fossil evidence had already pinned the transition from wolf to dog somewhere in Europe or Asia, and a 2002 study had shown that East Asian village dogs were more genetically diverse—an indication that wolves had first been domesticated in East Asia. But the Boykos' 2009 work found that the African village dogs were just as diverse as the East Asian ones. Some also carried a genetic signature shared with Middle Eastern gray wolves, supporting research by Robert Wayne and Bridgett vonHoldt of UCLA that points to the Middle East as the likely cradle of dogs.

The Boykos continue to expand their sample collection, with another expedition planned for Africa. And they've also begun using the same techniques to solve a related mystery: the strange disappearance of native dogs in South America. We know from the historical record that Native Americans had dogs. But previous population surveys in the Americas turned up only dogs with European heritage. "How do you ship so many dogs across the world that they completely replace the native dogs?" Boyko wonders, suspecting that in fact there may still be village dogs with native DNA in the remotest areas of the continent. So in August the three Boykos packed their bags and headed into the jungles of Peru, searching for the lost American dog. □

**Society Grant** Ongoing fieldwork on the native American dog DNA is funded in part by your National Geographic Society membership.

ALIDA LATHAM, DANITA DELIMONT