Biologists chase down pooches' genetic and social past

A Shaggy Dog History

Two-kilogram teacup poodles; 90-kg mastiffs; slender greyhounds; squat English bulldogs: For a single species, canines come in a vast array of shapes and sizes. Even more remarkably, they all come from the same stock. Many millennia ago, humans took in a few primitive wolves and made them man's best friend. Or so the story goes.

For centuries, researchers have doggedly pursued the evolutionary and social history of canines, with mixed success. Only subtle differences distinguish dogs from coyotes, jackals, and other canids, making family trees difficult to construct and the timing of the transition from wolf to dog hard to pinpoint. Archaeologists find both wolf and dog remains near ancient human camps, which leaves the date of domestication open to debate.

What seems certain is that dogs have been part of human history longer than cows, horses, or goats. And during that time, dogs have somehow adapted to their role as companions, developing sophisticated social skills not seen in other domesticated beasts. "Dogs have undergone a lot of selection to be compatible with humans," says Jennifer Leonard, now an evolutionary biologist at the Smithsonian National Museum of Natural History in Washington, D.C. "And the selection has really worked," she says. Just ask any dog owner.

In this week's issue of *Science*, three research teams chase down some of the age-old issues surrounding the evolution of dogs. Using genetic studies, one offers new evidence about where dogs were first domesticated; another employs DNA comparisons to show that New World pooches aren't from the New World at all; and the third evaluates the ability of dogs to follow human cues.

Some researchers think the results of these efforts clear up some key questions about dog evolution. "I'm very excited to read these articles," says John Olsen, an archaeologist at the University of Arizona in Tucson. But others are skeptical. "I am not sure I believe them," says Raymond Coppinger, a behavioral ecologist at Hampshire College in Amherst, Massachusetts, about the trio of reports.

Common pedigree. From Chihuahuas (*left*) to Great Danes, dogs of all shapes and sizes share common ancestors.

CREDIT: CHRIS ROGERS/CORBIS

An upcoming project might help resolve some of the continuing debates. In September, the National Human Genome Research Institute (NHGRI) put dogs high on the list of species whose genomes it will sequence. The sequence could provide new data not just for genetic research but also for evolutionary studies. The project "will certainly give us more information and will bring more attention to dogs," says I.Lehr Brisbin, a wildlife ecologist at the University of Georgia's Savannah River Ecology Laboratory in Aiken, South Carolina. "I am so excited that the dog has been picked."

Grandpaws

Dog researchers, whatever their pet theory, know they're in for a fight. "Everything that anyone publishes about the origin of the dog is controversial," explains Brisbin. "That's because everyone, even the man on the street, feels he is an expert on the dog."

Most enthusiasts agree with the standard story that dogs evolved from wolves. But a few insist that dogs stemmed, for example, from one of several jackal species, some hybrid canid, or even a contemporary of ancient wolves that has since gone extinct. Others have suggested that dog domestication took place more than once with more than one species, which might explain the great diversity seen in dog breeds.

Then there's the question of how domestication occurred. Some researchers think that early humans raised wolf puppies or tamed wolves as pets or possibly assistant hunters, selecting for ever-more-docile animals. But Coppinger and others think wolves, even as pups, don't have the right temperaments for a role in such a scenario. Coppinger and Brisbin assert that wolves became ever less fearful of people as they adapted to scavenging food from their two-legged neighbors. Thanks to this easy source of food, wolves born with greater boldness around humans thrived, eventually parting company with their more wary companions.

The date and place of domestication continues to be a mystery as well. Doglike jaws and other skeletal parts from 14,000 years ago have been discovered in central European and German sites. However, Italian researchers have suggested that their country is the dog's first home, citing DNA studies of 10,000- and 14,000-year-old wolf bones and 3500-year-old dog bones that show both these species had a genetic makeup similar to that of modern dogs.

Perhaps the most dramatic find comes from Israel: A woman was buried 12,000 years ago with what many believe is a puppy in her hands. Nearby, archaeologists found a man from the same era buried with two small canids, also presumably dogs. Coppinger is not swayed by these tableaux because the bones are too wolflike. But Tamar Dayan, an archaeologist at Tel Aviv University, points out that the specimens have some key dog characteristics, such as crowded teeth and shorter jaws. Furthermore, unlike other archaeological finds, "this is the one place where we have a whole group of animals all in the [right] cultural context" as companions to humans, she points out. She believes that truly domesticated dogs showed up first in Israel,

12,000 years ago. This approximate date was questioned some 5 years ago but is now coming back into favor.

Taming the DNA

Robert Wayne and Carles Vilà, evolutionary geneticists at the University of California, Los Angeles (UCLA), and their colleagues stepped into this fray with a publication in 1997. They hoped their genetic data would settle any controversy about both the ancestry of dogs and the date of their domestication. They succeeded—partially.

The researchers assessed differences in a section of the mitochondrial genomes of 140 dogs of different breeds from around the world: 162 wolves, five coyotes, and 12 jackals. "We showed very clearly that the dog is very close to the wolf and comes from several lineages of wolves," says team member Peter Savolainen, a molecular biologist at the Royal Institute of Technology in Stockholm, Sweden. Not everyone was convinced, but the work did tip the scales in favor of the wolf.

> **"It [was] evolutionarily beneficial [for dogs] to be able to read humans."**
> —Peter Savolainen

However, based on the number of differences between the sequences of wolves and dogs, the researchers estimated that dogs arose some 135,000 years ago—a conclusion that has quite a few colleagues growling. The date couldn't be right, opponents argue, given that the earliest accepted dog fossils date from just 14,000 years ago. They also suggest that very early humans were probably not sophisticated enough to keep wolves from interbreeding with dogs, a prerequisite for domestication.

While canine researchers were still debating Wayne and Vilà's 1997 results, Savolainen decided to pinpoint where domestication first occurred and perhaps take a second look at the earlier results. For this work, he studied mitochondrial DNA from 426 dogs from across the globe. In addition, he obtained data from studies of Chinese dogs: 100 samples analyzed and provided by Ya-Ping Zhang and Jing Luo of the Chinese Academy of Sciences in Kunming. The researchers also gathered DNA from 38 wolves from Europe and Asia.

As the previous study had found, most of the dogs and wolves fell into a single large genetically related group, and other dogs and wolves sorted into two medium-sized groups and several smaller ones. The three larger groups were distributed throughout Eurasia, suggesting that their ancestors had traveled extensively and mingled early in canine history. Furthermore, the data showed that similar breeds didn't arise from the same groups. Mastiffs and other large breeds didn't all fit, as one might have thought, into a single group that contained DNA from particularly large wolves.

Despite the different groups, the DNA samples were all similar enough that "we can say now there was probably one geographic origin," Savolainen concludes. That place was East Asia, he and his colleagues report on page 1610. The data aren't precise enough to identify a specific country, but "a good guess would be China," Savolainen says.

Several lines of evidence led Savolainen to East Asia. For one, he took a close count of the number of differences between the DNA of each group. As expected, he found that these differences had accumulated over time and had divided each group into subgroups. When he factored in the number of dogs in each group, he calculated that the East Asia pool had the most variety. "The high frequency of diversity in the East versus the West makes the [evidence] overwhelming," comments Brisbin. Furthermore, a large number of genetic sequences were found nowhere else but East Asia, suggesting that this population is ancient enough to have accumulated unique genetic signatures.

With these data, Savolainen and his colleagues also took a fresh look at the date-of-domestication question. Their estimate is 110,000 years later than that of Wayne and Vilà. But "we can't say for sure that one or the other is the right date," Savolainen points out, as even he can calculate a much earlier date depending on how he processes his data.

From the Old Country

Early dogs quickly became world travelers, new evidence suggests. When the first humans walked across the Bering Strait 10,000 to 15,000 years ago, dogs were by their sides, claims Leonard, who did this work at UCLA with Wayne, collaborating as well with Vilà, who is now at Uppsala University in Sweden. Until now, many people thought that dogs in the Americas were domesticated from New World gray wolves, but mitochondrial DNA studies tell a different story, she and her colleagues report on page 1613.

They decided to examine the origin of New World dogs because early genetic studies of supposed New World breeds showed rich European bloodlines. "It looked like the only way to address this was to look at archaeological specimens," she explains.

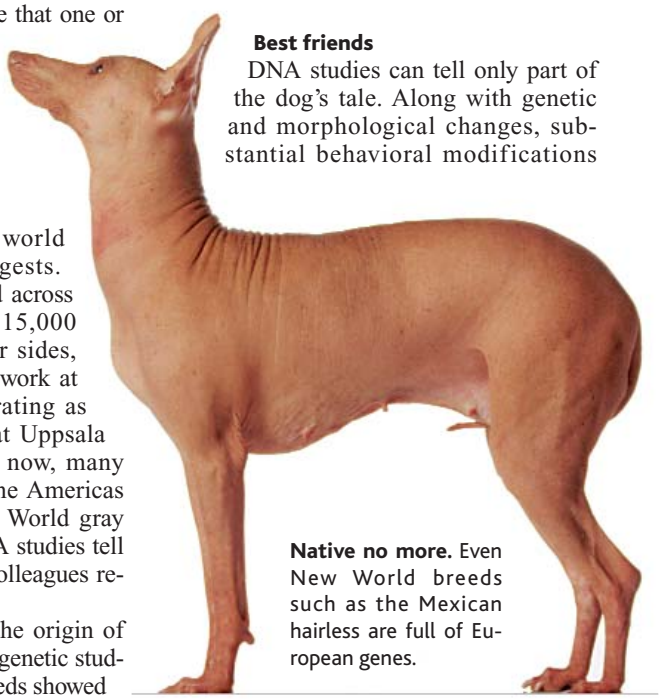
With the help of local researchers, the team studied 37 dog bones found at pre-Columbian archaeological sites in Mexico, Peru, and Bolivia. They extracted DNA from those samples and also looked at 11 DNA samples from dog remains deposited in Alaska before the arrival of the first European settlers. They compared these samples to DNA from 140 dogs and 259 wolves from around the world.

The ancient DNA was just like modern Eurasian dog DNA, the team found. New World dogs fell into the same branch of the canine family tree as three-quarters of the Old World dogs, a branch that includes so-called primitive dogs such as the Australian dingo, the African basenji, and the New Guinea singing dog. The American gray wolf proved to be just a distant cousin. It appears that "dogs accompanied humans into the New World," says David Hillis, an evolutionary biologist at the University of Texas, Austin. Moreover, the data suggest that five lineages of dogs came over the Bering Strait and became the predecessors of the Americas' dogs.

Finally, the results show that a second wave of fresh blood flooded into the New World canine community with the arrival of colonists millennia later. Even the Mexican hairless, Alaskan huskies, and the Newfoundland and Chesapeake Bay retrievers—all considered to be breeds that were developed in the Americas—have DNA sequences that are indistinguishable from those of modern European dogs, Leonard and colleagues report.

Best friends

DNA studies can tell only part of the dog's tale. Along with genetic and morphological changes, substantial behavioral modifications



Native no more. Even New World breeds such as the Mexican hairless are full of European genes.

CREDIT: YANN ARTHUS-BERTRAND/CORBIS

were produced over the course of domestication, and these likely cemented the dog's place by the fire. "To be able to live with humans, it [was] evolutionarily beneficial to be able to read humans," Savolainen points out.

On page 1634, Brian Hare, an anthropologist at Harvard University, and his colleagues demonstrate that a cognitive skill that dogs have—but nonhuman primates don't—evolved during domestication. This finding is important not just for understanding dog evolution but also for assessing how smart animals can be. "We tend to look at the primate work and if [primates] can't do it, we [assume] all animals can't do it," says Nicola Clayton, an ethologist at the University of Cambridge, U.K. But that just isn't so, says Hare's collaborator Michael Tomasello, a developmental and comparative psychologist at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany.

Our primate cousins can follow the gaze of other chimps or of humans and use that clue to find food behind a barrier. But other cues go right by them: After a researcher hides food in one of two containers, the chimp can't figure out the food's location if the researcher points to or taps on the container with the food.

That's not the case with dogs: Many take the hint the first time around, says Hare, who decided to see where this skill came from. Working with Christina Williamson of the Wolf Hollow wolf sanctuary in Ipswich, Massachusetts, Hare compared the success of seven human-reared wolves with that of seven dogs in picking the right container when he looked at, tapped, or pointed to it. All the containers smelled of food, so odor was not a cue. The dogs did significantly better than the wolves, he and his colleagues report. "I am quite convinced by their case that domestic dogs are absolutely expert at this thing," says Peter Marler, an ethologist at the University of California, Davis.

Next the researchers tried the experiment on puppies to determine whether the behavior was innate or learned. They used 32 puppies, aged 9 to 26 weeks. About half lived with families; the rest lived with one another in kennels and had little exposure to people. Many did quite well, and "there was no difference between those with a fair amount of experience in a home and those [with little experience with humans] in a kennel," says Tomasello.

Dog father. Dogs might have evolved from an ancestor of this Chinese wolf.

He and Hare conclude that these skills were selected during the transition from wolf to pet pooch and are now an innate part of the canine personality. But not everyone is convinced. Coppinger and others worry that the researchers can't control for how individual dogs or wolves react to the test situation, although Tomasello counters that they tested for relevant differences and found none. Nonetheless, Clayton is eager to see more work. "If it's the result of domestication that dogs have become particularly good at understanding human signals, then we expect there would be a whole battery of tests that they would be better at [than primates]," she points out.

Point and Play. Puppies can follow human cues to find food hidden under cups, a communication skill wolves lack.

Dogged pursuit

While Hare and Tomasello work out new tests of canine craftiness, their more genetically oriented colleagues are eager to pin down genes contributing the many different behaviors that dogs exhibit. This pursuit has a long history but until recently had seemed to stall.

Almost 50 years ago, two geneticists at Jackson Laboratory in Bar Harbor, Maine, began systematic studies of behavioral traits ranging from how well dogs get along with other dogs to their favorite play activity. John L. Fuller and John Paul Scott spent 20 years interbreeding basenji, cocker spaniels, Shetland sheepdogs, beagles, and wire-haired fox terriers. In one experiment, for example, the puppies were raised with minimal human contact, observed daily for 16 weeks, and evaluated according to their wariness toward people. From their observations, the researchers demonstrated that at least some aspects of behavior, such as aggressiveness, had a genetic basis. Moreover, they discovered that puppies passed through critical periods during which they learned specific behaviors, a realization that has guided dog training ever since.

Since then, behavioral studies have had their ups and downs. In 1990, Jasper Rine of the University of California, Berkeley, began trying to track down the genes involved in a Newfoundland's love of water and a Border collie's obsession with herding. He began building a genetic map to help with this quest. The breeding studies were discontinued for lack of funding, but Rine's colleagues continued the mapping project and now have a genetic map with 3400 landmarks on it, a resource that should speed the discovery of new genes. Now mappers Elaine Ostrander of the Fred Hutchinson Cancer Research Center in Seattle and her colleagues have convinced NHGRI that the dog warrants more attention from the genome-sequencing community.

This next step will enable researchers to explore why members of one species look and act so differently. "Of all the domesticated animals, the dog has been more artificially selected for divergent behavior than any other animal," Brisbin points out. "Having the genome sequenced is going to help us learn how those diverse behaviors are controlled genetically."

Such studies might also have biomedical benefits. Karl Lark, a geneticist at the University of Utah in Salt Lake City, is tracking down skeletal genes and their regulatory proteins in order to understand the vast array of canine sizes and shapes. He might uncover genes important in human skeletal abnormalities. But for Lark and others, the fascination lies in understanding the dog for the dog's sake. As Wayne points out, and every dog lover seconds, "there's really no other species like it."

–ELIZABETH PENNISI

CREDITS: (TOP TO BOTTOM) ZHINONG XI; SYLVIO TÜPKE