

How Wolf Became Dog

By Virginia Morell

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When you have cared for dogs and wild wolves from the time they are little more than a week old and have bottle-fed and nurtured them day and night, you are wise to their differences. Since 2008 Zsófia Virányi, an ethologist at the Wolf Science Center in Austria, and her colleagues have been raising the two species to figure out what makes a dog a dog—and a wolf a wolf. At the center, the researchers oversee and study four packs of wolves and four packs of dogs, containing anywhere from two to six animals each. They have trained the wolves and dogs to follow basic commands, to walk on leashes and to use their nose to tap the screen of a computer monitor so that they can take cognition tests. Yet despite having lived and worked with the scientists for seven years, the wolves retain an independence of mind and behavior that is most undoglike.

“You can leave a piece of meat on a table and tell one of our dogs, 'No!' and he will not take it,” Virányi says. “But the wolves ignore you. They'll look you in the eye and grab the meat”—a disconcerting assertiveness that she has experienced on more than one occasion. And when this happens, she wonders yet again how the wolf ever became the domesticated dog.

“You can't have an animal—a large carnivore—living with you and behaving like that,” she says. “You want an animal that's like a dog; one that accepts 'No!'”

Dogs' understanding of the absolute no may be connected to the structure of their packs, which are not egalitarian like those of the wolves but dictatorial, the center's researchers have discovered. Wolves can eat together, Virányi notes. Even if a dominant wolf flashes its teeth and growls at a subordinate, the lower-ranked member does not move away. The same is not true in dog packs, however. “Subordinate dogs will rarely eat at the same time as the dominant one,” she observes. “They don't even try.” Their studies also suggest that rather than expecting to cooperate on tasks with humans, dogs simply want to be told what to do.

How the independent-minded, egalitarian wolf changed into the obedient, waiting-for-orders dog and what role ancient humans played in achieving this feat baffle Virányi: “I try to imagine how they did it, and I really can't.”

Virányi is not alone in her bafflement. Although researchers have successfully determined the time, location and ancestry of nearly every other domesticated species,

from sheep to cattle to chickens to guinea pigs, they continue to debate these questions for our best friend, *Canis familiaris*. Scientists also know why humans developed these other domesticated animals—to have food close at hand—but they do not know what inspired us to allow a large, wild carnivore into the family homestead. Yet dogs were the first domesticated species, a status that makes the mystery of their origin that much more perplexing.

As inscrutable as the mystery is, scientists are piecing it together. In the past few years they have made several breakthroughs. They can now say with confidence that contrary to received wisdom, dogs are not descended from the gray wolf species that persists today across much of the Northern Hemisphere, from Alaska to Siberia to Saudi Arabia, but from an unknown and extinct wolf. They are also certain that this domestication event took place while humans were still hunter-gatherers and not after they became agriculturalists, as some investigators had proposed.

At what time and in what location wolves became dogs and whether it was only a one-time event are questions that a large research team, composed of once competing scientists, has just started to tackle. The researchers are visiting museums, universities and other institutions around the world to study collections of canine fossils and bones, and they are readying genetic samples from ancient and modern dogs and wolves for the most comprehensive comparison to date. When they are finished, they will be very close to knowing when and where—if not exactly how—wolves first began down the path toward becoming our trusted companions. Answers to these questions will complement the growing body of evidence for how humans and dogs influenced one another after that relationship was first forged.

Mixed signals

When modern humans arrived in Europe perhaps 45,000 years ago, they encountered the gray wolf and other types of wolves, including the megafaunal wolf, which pursued large game such as mammoths. By that time wolves had already proved themselves among the most successful and adaptable species in the canid family, having spread across Eurasia to Japan and into the Middle East and North America. They were not confined to a single habitat type but flourished in tundra, steppelands, deserts, forests, coastal regions and the high altitude of the Tibetan Plateau. And they competed with the newly arrived humans for the same prey—mammoths, deer, aurochs, woolly rhinoceroses, antelopes and horses. In spite of this competition, one type of wolf, perhaps a descendant of a megafaunal wolf, apparently began living close to people. For many years scientists concurred on the basis of small portions of the genome that this species was the modern gray wolf (*Canis lupus*) and that this canid alone gave rise to dogs.

But last January geneticists discovered that this long-held “fact” was wrong. Repeated interbreeding between gray wolves and dogs, which share 99.9 percent of their DNA, had produced misleading signals in the earlier studies. Such consorting between the two species continues today: wolves with black coats received the gene for that color from a dog; shepherd dogs in Georgia's Caucasus Mountains mate so often with the local wolves that hybrid ancestors are found in both species' populations, and between 2 and 3 percent of the sampled animals are first-generation hybrids. (Building on the admixture theme, in June researchers writing in *Current Biology* reported on the sequencing of DNA from a 35,000-year-old wolf fossil from Siberia. This species appears to have contributed DNA to high-latitude dogs such as huskies through ancient interbreeding.)

Analyzing whole genomes of living dogs and wolves, last January's study revealed that today's Fidos are *not* the descendants of modern gray wolves. Instead the two species are sister taxa, descended from an unknown ancestor that has since gone extinct. “It was such a long-standing view that the gray wolf we know today was around for hundreds of thousands of years and that dogs derived from them,” says Robert Wayne, an evolutionary geneticist at the University of California, Los Angeles. “We're very surprised that they're not.” Wayne led the first genetic studies proposing the ancestor-descendant relationship between the two species and more recently was one of the 30 co-authors of the latest study, published in *PLOS Genetics*, that debunked that notion.

More surprises may come from renewed efforts to nail down the timing and location of dog domestication. Previous studies left a confusing trail. The first analysis, carried out in 1997, focused on the genetic differences between dogs and gray wolves and concluded that dogs may have been domesticated some 135,000 years ago. A later study by some members of the same group indicated that dogs originated in the Middle East. But another analysis, which examined the DNA of 1,500 modern dogs that was published in 2009, argued that dogs were first domesticated in southern China less than 16,300 years ago. Then, in 2013, a team of scientists compared the mitochondrial genomes of ancient European and American dogs and wolves with their modern counterparts. It concluded that dogs originated in Europe between 32,000 and 19,000 years ago.

Evolutionary biologist Greger Larson of the University of Oxford, who is co-leading the recently launched multidisciplinary dog-domestication project, says the previous studies, while important, have shortcomings. He faults the 1997 and 2009 studies for relying solely on DNA from modern dogs and the last one for its geographically limited samples. “You can't solve this problem by using modern animals alone as windows to the past,” Larson says. The studies of modern dog DNA are not sufficiently informative, he explains, because people have moved and interbred dogs around the world numerous

times, blurring their genetic heritage. Any regional signatures that might have helped identify where they were domesticated has long since been lost.

To further muddy the picture, “wolves have a ridiculously broad distribution across the world,” Larson explains. In contrast, he points out, the ancestors of most other domesticated species, such as sheep and chickens, had much smaller geographical ranges, making it far easier to trace their origins.

Larson suspects that several geographically disparate populations of the ancestral wolf species may have contributed to the making of today's dog. It would not be the first time such a thing happened: Larson has shown that pigs were domesticated twice—once in the Near East and once in Europe. Intriguingly, enigmatic fossils from Belgium, the Czech Republic and southwestern Siberia that date to between 36,000 and 33,000 years ago and exhibit a mix of wolf and dog features hint at the possibility of at least three independent instances of domestication attempts from an ancestral wolf. But the anatomical characteristics of these fossils alone cannot answer the question of where dogs came from.

To solve the dog-domestication puzzle, Larson and his collaborators are using two key techniques employed in the pig study: they are undertaking a more thorough analysis of thousands of modern and ancient samples of dog and wolf DNA from individuals across the globe and are using a fairly new technique for measuring bones. Called geometric morphometrics, this method enables scientists to quantify certain traits, such as the curves of a skull, and so better compare the bones of individuals. Previously researchers relied primarily on the length of a canid's snout and the size of the canine teeth to distinguish dogs from wolves. Dogs' snouts are generally shorter, their canines are smaller, and their teeth are on the whole more crowded than those of wolves. The new method should identify other, perhaps more telling differences. Together these techniques should yield a far more detailed picture of dog domestication than any other approach has to date.

Close encounters

Although the when and where of dog domestication remain open questions, scientists now have a general idea of which kind of human society was the first to establish a close relationship with dogs. Perhaps not surprisingly, this question, too, has generated debate over the years. Some investigators have argued that settled agriculturalists had that distinction. After all, the other domesticated animal species all entered the human realm after people started farming and putting down roots. But other researchers credited earlier hunter-gatherers with being the first to have dogs. Wayne says that his team's latest DNA study has at last ended this part of the debate. “The domestication of the dog occurred prior to the agricultural revolution,” he asserts. “It happened when

people were still hunter-gatherers,” sometime between 32,00 and 18,800 years ago. (Agriculture is thought to have begun in a big way roughly 12,000 years ago in the Middle East.)

And that finding leads back to the questions Virányi and most everyone who owns and loves a dog has: How did these hunter-gatherers do it? Or did they? What if the first dogs—which, it is important to remember, would have at first been more wolf than dog—showed up on their own?

The genus *Canis* goes back about seven million years, and although some members of that group, such as jackals and the Ethiopian wolf, lived in Africa, the birthplace of humanity, there is no evidence that the earliest humans tried to domesticate any of these species. Only after modern humans spread out from Africa and into Europe 45,000 years ago did the wolf-dog-human triad begin to form.

Hints about the evolving relationship between canids and early modern humans have come from the paleontological and archaeological records. Take the canid remains unearthed between 1894 and 1930 at Přerost, a roughly 27,000-year-old settlement in the Bečva Valley in what is now the Czech Republic. The ancient people who lived and died there are known to us as the Gravettians, after a site with similar cultural artifacts in La Gravette, France. The Czech Gravettians were mammoth hunters, killing more than 1,000 of the great creatures at this one site alone. They ate the behemoths' meat, used their shoulder blades to cover human remains and decorated their tusks with engravings. They also killed wolves. Canids are the most abundant type of mammal at the site after mammoths, and their remains include seven complete skulls.

But some of the canid skulls do not look exactly like those of wolves. Three in particular stand out, says Mietje Germonpré, a paleontologist at the Royal Belgian Institute of Natural Sciences in Brussels. Compared with the wolf skulls found at Přerost, the three unusual ones “have shorter snouts, broader braincases and crowded teeth,” she notes.

These kinds of anatomical changes are the first signs of domestication, Germonpré and others say. Similar changes are found in the skulls of the silver foxes that are the focus of a famous, long-running experiment at Novosibirsk State University in Russia. Since 1959, researchers there have selected the foxes for tameness and bred them. Over the generations their coats have become spotted, their ears floppy, their tails curly, their snouts shorter and wider—even though the scientists have been selecting only for behavior. Similar changes are seen in other domesticated species, including rats and mink. Investigators have yet to explain why docile animals are consistently altered in these ways. They do know that the tame silver foxes have smaller adrenal glands and much lower levels of adrenaline than their wild counterparts.

Last year other scientists came up with a testable hypothesis: tame animals may have fewer or defective neural crest cells. These embryonic cells play a key role in the development of the teeth, jaws, ears and pigment-producing cells—as well as the nervous system, including the fight-or-flight response. If they are right, then all those cute domestic traits—spotted coats, curly tails, floppy ears—are a side effect of domestication.

Germonpré suspects that the apparent domestication at P^{re}redmostí was a dead-end event; she doubts that these animals are related to today's dogs. Nevertheless, to Germonpré, “they are dogs—Paleolithic dogs.” She says these early dogs probably looked very much like today's huskies, although they would have been larger, about the size of a German shepherd. Germonpré calls the P^{re}redmostí specimens “dogs” because of what she interprets as some type of relationship between the canids and the Gravettians. For instance, a dog's lower jaw was found near a child's skeleton, according to the diary of the original excavator.

The dogs were also included in rituals in ways that other species were not. In one case, a Gravettian tucked what is most likely a piece of mammoth bone between the front teeth of one of the dog skulls after the animal died and arranged its jaws so that they clamped together on the bone. Germonpré suspects that an ancient mammoth hunter placed the bone there as part of a ritual related to hunting, or to help sustain in death an animal the hunter revered, or to enable the dog to assist a human in the afterlife. “You see this kind of thing in the ethnographic record,” she says, citing, as one example, a Chukchi ceremony in Siberia for a deceased woman in the early 20th century. A reindeer was sacrificed and its stomach placed in the mouth of a dead dog's head, which was then positioned to protect the woman on her death journey.

Many researchers imagine that these early people set about making the wolf into the dog to help us hunt big game. In her book *The Invaders*, published by Harvard University Press earlier this year, anthropologist Pat Shipman argues that the first dogs (or wolf-dogs, as she calls them) were like a new and superior technology and helped the mammoth-hunting modern humans outcompete the Neandertals. But she, Wayne, Larson and others think that wolves joined forces with humans on their own; that the canny, adaptable canids identified us as a new ecological niche they could exploit. The alternative scenario—people brazenly raiding wolf dens to steal pups young enough for taming—would have been a dangerous undertaking. And raising wolves in camps with young children would have presented another serious risk.

“We didn't do [domestication] deliberately; not at first,” Larson surmises. Instead wolves most likely started following people for the same reason that ants trail into our kitchens—“to take advantage of a nutritional resource, our trash.” Over time, some of these camp-following wolves increasingly lost their fear of people—and vice versa—and

a mutually beneficial relationship developed. Wolf-dogs would sniff out prey for us, and we would share the resulting meat with them. (Circumstantial evidence for this scenario comes from the silver fox experiment. By selecting foxes that were less fearful of humans, the researchers at Novosibirsk eventually developed a silver fox that runs to greet people. Most silver foxes in captivity hide in the back of their cage.)

There is just one problem with this imagined event, at least at P[~]redmostí: Germonpré's early dogs were not eating mammoth meat even though that is what the humans were dining on; isotopic analysis of the Paleolithic dogs' bones indicates that they were eating reindeer, which was not a favored food of the people who inhabited the site. The P[~]redmostí dogs also had broken teeth and severe facial injuries, many of which had healed. "Those could be signs of fighting with other dogs," Germonpré says, "or of being hit with sticks." She pictures the human-dog bond developing via the mammoth hunters' canid rituals. In this scenario, the hunter-gatherers brought pups to their camps, perhaps after killing the adult wolves, just as many modern nomadic peoples bring baby or young animals to their settlements. The mammoth bones at P[~]redmostí show no signs of being gnawed by canids, which suggests they were not free to roam and scavenge people's scraps. Rather humans probably tied the canids up, fed them what appears to have been second-rate food, given that the humans were not eating it, and even bred them—all to ensure a ready supply of victims for their ritualistic sacrifices.

Breeding wolves in captivity would lead to the anatomical changes that Germonpré has documented in the P[~]redmostí dogs and could even produce a less fearful and independent animal as seen in the Novosibirsk silver foxes.

Confined, beaten, fed a restricted diet, the dogs at P[~]redmostí would likely have understood the meaning of "No!" There is no evidence at P[~]redmostí or other comparably old sites where dog remains have been uncovered that the ancient hunter-gatherers there regarded the canines as their friends, companions or hunting pals, Germonpré observes. "That relationship came later."

Shifting fortunes

If Germonpré is right, then dog domestication may have begun quite early and under circumstances that were not favorable for the dogs. Not every scientist agrees that Germonpré's dogs are dogs, however. Some prefer the wolf-dog designation or simply "wolf" because their taxonomic status is not clear either from their morphology or genetics. (Larson expects to resolve this question over the course of his mega project.)

The earliest undisputed dog on record, a 14,000-year-old specimen from a site called Bonn-Oberkassel in Germany, tells a very different story of dog domestication, evincing a much more affectionate bond between humans and canines. In the early 1900s

archaeologists excavating the site found the dog's skeleton interred in a grave with the remains of a man about 50 years old and a woman about 20 to 25. When researchers see such associations, they know they are looking at a fully domesticated animal—one that is treasured and regarded so highly that it is given a burial as if it, too, were a member of its human family.

The Bonn-Oberkassel dog is not the only ancient hound to have received such honors. In Israel, at Ain Mallaha, a hunter-gatherer site dating to 12,000 years ago in the upper Jordan Valley, archaeologists discovered what is perhaps the most famous dog-human burial. The skeleton of an elderly person lies curled on its right side, its left arm stretched out under the head, with the hand resting gently on a puppy. The dog was about four to five months old and was placed there, archaeologists think, to be a companion to the deceased. Unlike the P^{re}redmostí dogs, this puppy was not battered; its remains were arranged lovingly with someone who may have cared for it.

Although such touching dog-human scenes are rare during this period, dog burials are not. And after about 10,000 years ago, the practice of entombing dogs increased. No other animal species is so consistently included in human mortuary rituals. People had come to see dogs in a different light, and this shift in attitude had a profound effect on dogs' evolution. Perhaps during this period dogs acquired their human social skills, such as abilities to read our facial expressions, understand our pointing gestures and gaze into our eyes (which increases oxytocin—the love hormone—in both dog and owner).

“Dog burials happen after hunting moves away from the open plains and into dense forests,” says Angela Perri, a zooarchaeologist at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and a specialist on these burials. “Dogs in open environments might be good for helping you transport meat from killed mammoths but wouldn't necessarily help you hunt them,” she says, noting that elephant hunters do not use dogs. “But dogs are excellent for hunting smaller game, such as deer and boar,” that live in forests.

Beginning at least 15,000 years ago and probably somewhat earlier, Perri says, hunter-gatherers in Europe, Asia and the Americas began depending on their dogs' hunting skills for survival. Researchers cannot trace a direct genetic line from those animals to our pet pooches; nevertheless, they say, these animals were unquestionably dogs. “Good hunting dogs can find fresh tracks, and guide the hunters to the prey, and hold them at bay,” says Perri, who has joined traditional hunters and their dogs in Japan and the U.S. “When people start using dogs for hunting, you see a switch in how people view them, and you start finding dog burials across the world.” Such burials are not rituals or sacrifices, she emphasizes. “These are burials of admiration, where the dogs are interred with ocher, stone points and blades—male tools of hunting.”

One of the most elaborate dog burials comes from Skateholm, Sweden, and is dated to about 7,000 years ago. Several dogs were found interred in the same area with dozens of humans. One was particularly celebrated and given the finest treatment there of anyone, human or dog. “The dog was laid on its side, flint chips were scattered at its waist, and red deer antlers and a carved stone hammer were placed with it, and it was sprinkled with red ocher,” Perri says. There is no indication of why this dog was so revered, but she suspects it must have been an excellent hunter and that its human owner mourned its death. “You see this relationship among hunters and their dogs today and in the ethnographic record,” Perri observes, noting that Tasmanian hunter-gatherers in the late 19th century were quoted as saying, “Our dogs are more important than our children. Without them, we couldn't hunt; we wouldn't survive.”

Early dogs provided other important services, too. The first known attempt at the kind of intentional selection that has shaped the evolution of *C. familiaris* comes from a site in Denmark dating to 8,000 years ago. The ancient hunter-gatherers there had three sizes of dogs, possibly bred for certain tasks. “I didn't expect to see something like dog breeds,” Perri says, “but they had small, medium and large dogs.” It is not clear what they used the small dogs for, but the medium-sized animals had the build of hunting dogs, and the larger ones, which were the size of Greenland sled dogs (about 70 pounds), most likely transported and hauled goods. With their warning barks, all the dogs would have served as camp sentinels, too.

The dog's status plunged when people developed farming. In early agricultural settlements, dog burials are rare. “The difference is so strong,” Perri says. “When people are living as hunter-gatherers, there are tons of dog burials.” But as agriculture spreads, the burials end. “Dogs are no longer as useful.” That fall from grace, though, did not doom them to extinction—far from it. In many places, they began to turn up on the dinner table, providing a new reason to keep dogs around.

Not all agricultural cultures consigned Fido to the menu, however. Among those groups that tended livestock, dogs were sometimes bred for herding. Those that proved their worth could still end up pampered in the afterlife. In 2006 archaeologists discovered 80 mummified dogs buried in graves next to their human owners at a 1,000-year-old cemetery near Lima, Peru. The dogs had protected the Chiribaya people's llamas and, in return for their service, were well treated in life and death. Nearly 30 of the dogs were wrapped in finely woven llama-wool blankets, and llama and fish bones were set close to their mouth. The region's arid climate mummified the dogs' remains, preserving their fur and tissue. Unwrapped, the mummies resemble the small street dogs that roam Lima today, looking for a human to take them in and tell them what—and what not—to do. (That resemblance notwithstanding, the Chiribaya herding dogs are not related to Lima's modern-day mutts. Nor is there any evidence to support claims linking any of the

breeds of antiquity anywhere to the modern, standard breeds of the American Kennel Club.)

Although the Chiribaya dogs and other dog burials in the Americas hail from the wrong place and time to represent the earliest stages of domestication, Larson and his colleagues are happily measuring their bones and sampling their DNA. That is because these early North American dogs descended from ancient European or Asian dogs; their bones and genes will help the scientists determine how many dog-domestication events occurred and where they took place. Thus far in their attempt to study as many ancient canids as possible, the researchers have analyzed upward of 3,000 wolves, dogs and other specimens that do not readily fall into either box. More than 50 scientists worldwide are helping with the effort. They expect to have a paper ready on their initial findings by this summer.

Will we then finally know where and when the dog became domesticated? “I expect we’ll be very close to an answer,” Larson says. But we still won’t know exactly how some long-lost type of wolf managed to become a creature that respects “No.”

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