The Woof at the Door

Pat Shipman

IT'S FUNNY HOW MUCH difference a single letter makes. A "woof" at the door is a very different thing from a wolf at the door. One is familiar, domestic, reassuring; the other is a frightening apparition of imminent danger. The distinction between our fond companions and the ferocious predator of northern climes goes back a long way.

Dogs are descended from wolves, probably the gray wolf. Some scientists argue that, because dogs and wolves can and do interbreed, they shouldn't be considered to be separate species at all. They believe that domestic dogs are only a subspecies or variant of the gray wolf, *Canis lupus*, and ought to be called *Canis lupus familiaris (*the familiar or domestic wolf) instead of *Canis familiaris* (the familiar or domestic dog). Although the ability to interbreed and produce fertile offspring is a tried-and-true criterion for recognizing that two populations are really variants of a single species, the reality is more nuanced. We cannot know whether dog-wolf hybrids will thrive and survive, or die out, in the long run.

Certainly we expect to be able to distinguish a dog from a wolf if we see one. Of course, domestic dogs are wildly variable in size and shape, thanks to several hundred years of selective breeding. Some have long, fluffy coats; others have tightly curled, nearly waterproof coats and webbed feet. Some are leggy and swift, whereas others are solid, stoutly built guard dogs. Some fit neatly into a pocketbook, but others barely fit into a compact car. As Robert K. Wayne of the University of California at Los Angeles declares, "Dogs show more diversity in appearance than any other mammal."

What is it that tells us this animal is "dog" and that one is "wolf?"

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> *Dogs may have been man's best friend for thousands of years longer than we realized*

Modern wolves and dogs can be distinguished reasonably easily by their appearance. The most telling feature of dogs is the snout, which is significantly shorter and wider than wolves' snouts. Only a few dog breeds with extremely elongated, slender snouts, such as Irish wolfhounds, surpass wolves in "snoutiness."

But a crucial part of the difference we perceive is in the animals' manner and attitude towards humans. Domesticated dogs are just that: canids that live in the house or domicile of humans. They are genetically disposed to seek out human attention and approval and to accept human leadership. Wolves are not.

How did this important change come about? Probably in the distant past, humans took in a wolf cub, or even a whole litter of cubs, and provided shelter, food and protection. As the adopted cubs matured, some were aggressive, ferocious and difficult to handle; those probably ended up in the pot or were cast out. The ones that were more accepting of and more agreeable to humans were kept around longer and fed more. In time, humans might have co-opted the natural abilities of canids, using the dogs' keen noses and swift running skills, for example, to assist in hunting game. If only the most desirable dogs were permitted to breed, the genes encoding for "better" dogs would continue to be concentrated until the new domesticated species (or subspecies) was formed.

Time to Tame

The creation of a domestic, useful, familiar canid by years of selectively breeding wild and terrifying wolves was almost certainly unplanned. The wolf at the beginning of the process of domestication was tamed—made individually docile—but the essential fact is that, over time, the offspring of those initial wolves were genetically inclined to be more tractable.

Domestication was one of the most brilliant accidents in the entire history of humankind. What's more, we got it right the first time: Dogs were the original trial animal, and successful product, of such an accident—the happy outcome of years of unwitting experiments and dumb luck.

How long does domestication take? Nobody knows. In an experiment, Russian biologists kept a breeding colony of silver foxes and intentionally selected for breeding those with the least fear and the least aggression toward humans. After 10 generations, 18 percent of the foxes sought human contact and showed little fear. After 30 or so generations, a "domesticated fox" had been created.

The catch is that this experiment was deliberate and strictly controlled. The foxes could not breed with wild foxes and dilute the changing gene pool. Human contact was minimized so animals could not be tamed by their handlers. And because of the experiment's scientific intent, no one could say, "Oh this one is so cute, let's let it breed even if it is a little aggressive." So in the case of dogs, without all these controls, the process could have taken much longer.

Another way of estimating the time at which domestic dogs originated is to consider their genetic differences from wolves. One prominent group of researchers, including Robert Wayne, along with Carles Vilà of the Uppsala University in Sweden and their collaborators, initially estimated in 1997 that dogs diverged from gray wolves 100,000 to 135,000 years ago. After more study,

they revised their divergence date to between 40,000 and 100,000 years ago. Another group, led by Peter Savolainen of the Royal Institute of Technology in Sweden, favored the Chinese wolf, a subspecies of the gray wolf, as the probable ancestor and estimated in 2002 that it was domesticated between 15,000 and 40,000 years ago.

How do these genetic estimates stack up against the fossil record? Until 2009, the oldest known remains of domestic dogs were two adult skulls dated to between 13,000 and 17,000 years ago, from Eliseevichi, a region in Russia. Both had the relatively broad, short snout typical of dogs, and both were large, heavy animals, nearly the size of great Danes.

Then a team led by Mietje Germonpré of the Royal Belgian Institute of Natural Sciences reported a stunning new finding in the February 2009 issue of *Journal of Archaeological Science:* a nearly complete fossil dog skull dated to 31,680 ± 250 years ago.

Paul Bahn

Prehistoric cave paintings rarely depict wolves or other carnivores. This watercolor tracing of a cave painting was made by the archaeologist Abbé Henri Breuil in the early 1900s from the Grotte de Font-de-Gaume in France. The 17,000-year-old cave paintings number about 250 and mostly show bison and mammoths—only one is thought to be a wolf. Canids may have been domesticated by this point; it is possible that portraying wolves and humans was taboo.

Another Look

Germonpré and her colleagues thought that researchers might have overlooked early prehistoric dogs in the fossil record of the Upper Paleolithic, so they analyzed skulls of large canids (wolves or dogs) from various European sites. The Upper Paleolithic time period spanned 40,000 to 10,000 years ago and is divided into sections based on the artifacts from those times. By convention, each span is named for a culture of people who made the artifacts, and the people, in turn, are usually named for the geographical location where the artifacts were found. The Epigravettian culture existed from 14,000 to 10,000 years ago; before that, the Magdalenian culture thrived from 18,000 to 10,000 years ago; and skipping back a few sections, the Aurignacian culture occurred from 32,000 to 26,000 years ago.

In order to identify the fossil skulls accurately, Germonpré's team first analyzed a large reference sample of 48 wild, modern wolves and 53 dogs belonging to 11 different breeds. They also examined five skulls (including the ones found in Eliseevichi) that were firmly established as prehistoric domesticated dogs.

The team used statistical analysis of cranial and dental measurements on the skulls to sort the reference sample into six natural clusters. One cluster contained modern wolves. Another consisted of recent dogs of archaic proportions (such as chow-chows and huskies); a single specimen of a Central Asian shep-

herd was closer to this group than any other but fell outside it. A third cluster included dogs, such as German shepherds and malinois, which have wolflike proportions. These three groups overlapped each other in their cranial proportions. A fourth group of modern dogs has short toothrows—the length of the jaw that contains teeth—and includes such breeds as great Danes, mastiffs and rottweilers. This group overlapped slightly with the archaic-proportioned dog group but not with the others.

The fifth and sixth clusters were completely separate from all others. One consisted of dogs with extremely long, slender snouts, such as Doberman pinschers. The final group, which had long toothrows and short, broad snouts, was made up of the prehistoric dogs. Statistically, the team's ability to identify any individual specimen as belonging to the correct group was highly significant and accurate.

Using these clusters as reference categories, Germonpré and colleagues used a statistical technique (called *discriminant function analysis*) to assign 17 unknown fossil canid skulls to the established categories. Not all of the "unknowns" were truly unknown, however. Five were immature modern wolves that might have had different proportions because of their age, two were wolves that had been kept in captivity, and one was the Central Asian shepherd that didn't cluster into any of the groups. Additional

unknowns were 11 fossil skulls from sites in Belgium, the Ukraine and Russia, although two of these fossil skulls proved to be too incomplete to classify.

The technique correctly classified all of the immature wolves as wolves, but the two zoo wolves were classified as recent dogs with wolflike snouts. Five of the fossil skulls also fell easily into the modern wolf group; although two of these specimens fell into the region of measurements that overlapped with the group of recent dogs with wolflike snouts, they had a higher statistical probability of being wolves. One fossil skull fit directly into the group of recent dogs with wolflike snouts, even though this specimen was clearly ancient.

The remaining three fossil skulls—one from Goyet Cave in Belgium and one each from Mezin and Mezhirich in the Ukraine—resembled each other closely. All three were classified as prehistoric dogs with probabilities of 99 percent, 73 percent and 57 percent, respectively, as was the (modern) Central Asian shepherd, with a 64 percent probability. In addition, the Mezin skull was odd enough in appearance (for a wolf) that another researcher has suggested it might have been a captive wolf. Germonpré and her team were delighted with these results.

The group also successfully extracted mitochondrial DNA (mtDNA) from seven ancient canid bones from Goyet Cave and Trou des Nutons in Belgium. Rather than damage precious skulls, they
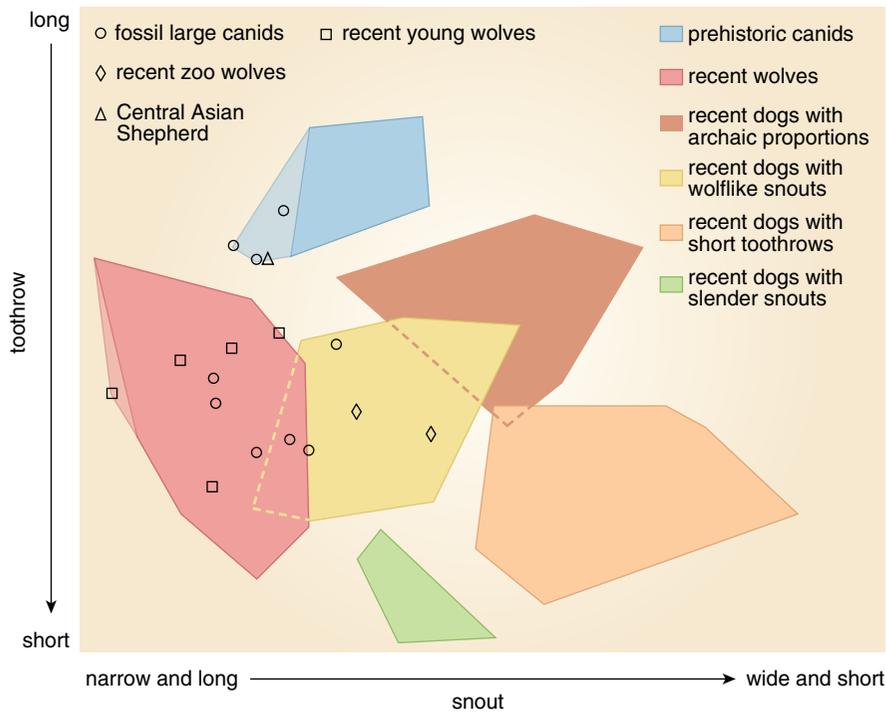
In order to establish the morphological differences between wolves and dogs, a group of researchers led by Mietje Germonpré statistically analyzed skulls from 48 modern, wild wolves and 53 modern dogs from 11 breeds, as well as five skulls that were previously established to be from prehistoric dogs. Recent wolves *(purple)* and prehistoric dogs *(blue)* clustered into their own groups, based on the length of their toothrows and the shape of their snouts. Modern dogs clustered into four groups, with some overlap in their areas. Recent dogs with archaic proportions included huskies *(pink)*, recent dogs with wolflike snouts included German shepherds *(yellow)*, recent dogs with short toothrows included great Danes *(orange)*, and recent dogs with slender snouts included doberman pinscers *(green)*. One modern dog, a Central Asian shepherd, clustered with the prehistoric dogs. The group then classified new skulls into the established groupings; examples that fell slightly outside of the ranges but that are statistically likely to be within the group are shown as lighter-shaded areas. Recent young wolves fell into the recent-wolf group, whereas wolves kept in captivity were classifed as recent dogs with wolflike snouts. Fossil canid skulls divided between the recent-wolf group and the prehistoric-dog group, with one falling in the group of recent dogs with wolflike snouts. Data courtesy of Mietje Germonpré.

sampled only bones in which wolves and dogs differ little, so they presumed all of those they sampled for mtDNA were wolves. From each sample, they sequenced a segment of the mtDNA that is highly variable in living wolves and dogs. Each fossil had a unique mtDNA sequence, or *haplotype*, in this region, which could not be matched with any known sequences for modern wolves (of which there are about 160) or modern dogs (of which more than 1,000 exist) stored in GenBank, a database of all publicly available nucleotide sequences.

"I was not so surprised at the rich genetic diversity of the fossil wolves," says Germonpré, because there have been other studies with similar findings. Foxes and wolves underwent a severe bottleneck in population size at the end of the last Ice Age, and many genetic lineages went extinct at this time.

"But we *were* surprised at the antiquity of the Goyet dog," Germonpré adds. "We expected it would probably be Magdalenian," perhaps 18,000 to 10,000 years old. This outcome would fit with their results for the Mezin and Mezhirich skulls, which were found with Epigravettian artifacts roughly 14,000 to 10,000 years old. When the age of this specimen from Goyet was directly dated using accelerated mass spectroscopy radiocarbon-dating techniques, the team found that it was not 18,000 years old, but almost twice as old as the next oldest dog, placing the Goyet dog in the Aurignacian period.

A Time of Change

The Goyet dog fossil shows that the domestication of the first animal was roughly contemporaneous with two fascinating developments in Europe.

Around this time, Europeans began producing objects that are recognizable as art. Some of the earliest known art objects from Europe include the remarkable cave paintings of Chauvet Cave in France, the oldest of which were made 32,900 ± 490 years ago. None of the hundreds of glorious Chauvet paintings show wolves. However, the cave preserves something even more

Around 33,000 years ago, humans began perforating teeth for use in decoration. Although canid teeth made up a very small percentage of the total fauna teeth available, they were used in a majority of the ornaments. Fangs from foxes and wolves appear to have been favorites. One example of a perforated wolf tooth *(shown in two views at right)* is from Abri Castanet in France and has been dated to 33,000 years ago. A strand of beads interspersed with fox teeth came from the Russian site of Sungir and has been dated to 24,000 years ago *(left)*. There is no specific evidence that canid teeth were used in necklaces; the fox-teeth strand may have been a belt.

haunting: the footprints of a human child about four-and-a-half feet tall, as well as many footprints of large canids and bears.

Michel-Alain Garcia of the Centre National de la Recherche Scientifique in Nanterre noticed in 1999 that one track of canid prints appears to accompany the child's prints. These canid prints, unlike the others, have a shortened middle digit on the front paw: a characteristic of dogs. Garcia suggested that the child and dog might have explored the cave together. Charcoal from a torch the child carried is 26,000 years old.

The Upper Paleolithic cultures of Europe are famous for the flowering of all kinds of exquisite art: sculptures, carvings, paintings and engravings. Animals are common and readily recognizable subjects. Prehistoric art expert Paul Bahn notes that depictions of carnivores, including wolves or dogs, and of humans are rare. Bahn conjectures that portraying wolves and humans might have been taboo.

Anne Pike-Tay of Vassar College offers another perspective. She observes that the scarcity of artistic depictions of carnivores parallels their scarcity in the fossil faunas of the Upper Paleolithic. If domesticated dogs were helping humans hunt, she speculates that they might have been placed in a completely different symbolic category from other animals.

"What if dogs were put in the 'human family' category as an extension of the hunter, and like humans, warranted no (or very few) painted or engraved depictions?" she wonders.

The second development of the Aurignacian period is the appearance of objects of personal adornment: jewelry. Although beads and perforated objects occurred much earlier in Africa, the earliest such objects in Europe appeared about 40,000 years ago. At 33,000 years ago, early Aurignacian people began perforating animal teeth (and occasionally human teeth) to wear as pendants or other ornaments, such as belts.

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Fossils have helped to establish a far earlier timeframe for dog domestication. A paleolithic canid skull from Goyet in Belgium, about 31,000 years old, has traits characteristic of a dog rather than a wolf *(a)*. **When compared to wolves from a similar era, one from Trou Ballu** *(b)* **and one from Trou des Nutons** *(c)* **in France, the Goyet dog has a relatively wider snout and larger carnassial teeth, and it also has a wider braincase.**

Which teeth did they choose? Among their favorite sources are what have been identified as fangs of foxes and wolves. These identifications might better be termed "small or large canids," because until now no one has considered the possibility that dogs might have been domesticated so long ago. Besides, identifying a single canid tooth specifically as dog or wolf would be difficult, if not impossible.

Randall White of New York University argues that Aurignacian and later people chose to wear objects that displayed their identity or membership in a certain group or clan. Like gang colors or a t-shirt that proclaims its wearer to be a fan of a particular band, ancient people wore things that made their allegiances clear.

White observes that the teeth Aurignacian people chose to wear were obviously not a random sample of the animals in the fauna. For example, the fauna from

the Grotte des Hyènes (Cave of Hyenas) at Brassempouy, France, is dominated by horses, aurochs (a type of cattle) and reindeer—mostly as food remains that often show cutmarks or charring—as well as hyenas, which probably lived in the cave when humans did not. Wolves are rare, making up less than 3 percent of the total fauna. Of approximately 1,600 animal teeth at Brassempouy, only about 2 percent were modified for use as ornaments. However, nearly two-thirds of the ornaments are teeth of wolves or foxes. The rest of the perforated teeth are from other rare species: bear, humans and red deer. None of the teeth of the most common species were used as ornaments at Brassempouy.

Did someone who wore a perforated canid tooth 33,000 years ago proclaim him- or herself to be one of the group that domesticated dogs?

Possibly. Domesticating dogs was a remarkable human achievement that doubtless provided a definite selective advantage to those who accomplished it successfully. They might well have had reason to brag about their accomplishment by wearing canid teeth.

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