EVOLUTIONARY BIOLOGY

The Origin of Dogs: Running With the Wolves

Like the latest batch of Nike shoes, dogs today come in just about every size, shape, and color imaginable. Indeed, their variation is so great—from pocket-sized Chihuahuas to mighty St. Bernards to long, lean dingoes—that Charles Darwin and others once thought dogs may have descended from a mixture of wild canids, including the jackal. But as an international team of geneticists and evolutionary biologists reveals on page 1687 of this issue, all of today's breeds had only one canine forebear: the wolf. What's more, the team, led by Robert Wayne of the University of California, Los Angeles, says that although humans tamed members of that lone progenitor species at least twice, domestication was apparently a relatively rare event, requiring special skill.

ALL PHOTOS FROM ANIMALS/ANIMALS

MICHAEL DICK

The researchers also say that the first transformation from wolf to dog may have happened more than 100,000 years ago—long before the 14,000-year date archaeologists typically assign to Fido's domestication. Many biologists remain skeptical about the date, but they are impressed by the genetic study, the largest of its kind for the dog. "That's absolutely great; it's first-rate," says Stephen O'Brien, a geneticist and chief of the Laboratory of Genomic Diversity at the National Cancer Institute in Frederick, Maryland, who has done similar genetic studies of wild and domestic cats. "He has confirmed genetically what most zoologists have believed for a long time," adds David Mech, a wolf expert with the Department of the Interior in St. Paul, Minnesota, "and that is that the dog is a domesticated wolf."

R. & E. PEARCY

To prove that even a toy poodle is a wolf in dog's clothing, evolutionary biologist Wayne and his team amassed tissue samples from 162 wolves from North America, Europe, Asia, and Arabia, as well as from 140 dogs representing 67 breeds and five mixed breeds. They also sampled coyotes and jackals, because all wild canids can mate and so might have contributed their genes to the making of man's best friend. From these tissues (taken from wild and captive animals, as well as museum specimens), Wayne's lab sequenced the DNA in the canids' mitochondria, which is inherited only from the mother. Wayne studied a stretch of mitochondrial DNA known as the control region, which in mammals is known to have a high mutation rate and so would be likely to reveal differences between closely related animals such as wolves and dogs.

The team found a total of 27 different haplotypes, or particular sequences, in the wolf control region and 26 sequences in the dog. The dog haplotypes did not sort by breed—that is, individuals of the same breed might carry different haplotypes, indicating a diverse ancestry. So—breeders' statements aside—there may be no such thing as a "pure" dog breed, notes Wayne.

PETER WEIMANN

M. & B. REED

Honey, I shrunk the wolf. The wolf *(above)* gave rise to all of today's dog breeds, including (clockwise from top right) the St. Bernard, elkhound, Mexican hairless, pug, and New Guinea singing dog.

But all the dog sequences clearly differed from jackals and coyotes in at least 20 sites, where one nucleotide was substituted for another. And all the wolf and dog sequences were similar, differing by at most 12 substitutions. That clearly indicates the wolfish ancestry of all dogs, says Wayne. Because the study used mitochondrial DNA, it could have missed the contributions of wild male jackals that might have mated with female dogs. But Wayne's lab also has done a smaller study of nuclear DNA that gave the same results.

Next, Wayne's group explored the relationships among the haplotypes, using several phylogenetic methods to lump the wolf and dog sequences into clades, or groups. Regardless of the method, all the dogs' haplotypes fell into four distinct clades. In two of these, the sequences showed that the dogs came from two unique common ancestors. Thus, each of these clades was founded by a separate wolf population. This in turn implies two separate domestication events, as people isolated dogs from wolves and so created each clade, explains Wayne. The other two clades include some wolf haplotypes, indicating that on two subsequent occasions, wolves were either brought in to mate with dogs, or dogs mated with their wild forebears, says Wayne. Clade I, the largest of the four, contains 19 out of the 26 dog haplotypes, suggesting that some three-quarters of modern dogs (including all members of a few ancient breeds such as greyhounds and New Guinea singing dogs) stem from a single female lineage and a common domestication.

RALPH A. REINHOLD

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Wayne tried to genetically link that vast group of dog sequences to particular wolf populations living today, but he could not find a match. Thus, the actual wolf progenitor remains "a mystery," says Wayne. Although he sampled as many wolves as possible, it may be that the ancestral wolf population is now extinct, he says.

Finally, Wayne and colleagues tackled the question of timing. The number of nucleotide differences in similar DNA sequences from various species can serve as a molecular clock, showing how much time has passed since the species last shared a common ancestor. Wayne's team calibrated their mitochondrial clock based on the sequence differences between wolves and coyotes, which parted ways a million years ago according to the fossil record; during that time, 7.5% of their mitochondrial sequence changed. When applied to Clade I, that clock yields a date of 135,000 years for the separation of dogs from wolves. Even Wayne admits that the date could be far younger, because mitochondrial sequences have notoriously high and uneven rates of change. Still, he argues that the diversity of the mitochondrial sequences in Clade I implies that the real date is much earlier than archaeologists have thought. "It takes far more than 14,000 years to create a clade with that much diversity and that shares a single common ancestor," he says.

It's not just the diversity of the dogs' sequences, but also the fact that any wolf sequences have been lost from Clade I that points to an early date, says Dan Bradley, a molecular evolutionist at Trinity College, Dublin in Ireland. "That big clade is genetically and geographically diverse, and yet it is *all* dogs; there are no wolves in it. And that does not fit the idea of a single domestication of the dog only 14,000 years ago."

The absence of wolf sequences in Clade I also implies that once humans domesticated dogs, they interbred them with other dogs rather than seeking out fresh genetic stock in wild wolves, says Wayne. "It suggests that it takes some special skill to domesticate a wolf. If it were more easily done, you'd find more sequences similar to wolves in the dog clades." That fits an emerging pattern that the taming of wild animals is a fairly rare event requiring particular skill. For example, Bradley has shown that cattle were domesticated twice, while other research indicates that chickens were tamed only once.

Many scientists are quite skeptical of Wayne's estimated date, however. "It's a fascinating suggestion, saying that dogs are 10 times older than we thought," says Svante Pääbo, a molecular geneticist at the University of Munich in Germany. But he and others caution that the mitochondrial clock is none too reliable. "The date is very dubious—it's 135,000 years plus or minus about 300%," says O'Brien. Those who study the archaeological record are even more doubtful. Says paleoanthropologist Richard Klein of Stanford University, "There are no animal bones suggesting domesticated dogs—or domesticated anything—remotely approaching that time."

Wayne and his colleagues suggest that dogs aren't seen in the archaeological record until 14,000 years ago because they looked like wolves before that date. Dogs, they propose, may not have become morphologically distinct from wolves—becoming smaller and shorter muzzled—until humans themselves settled down in agricultural communities. That might mean that wolf bones from some early hominid sites are actually those of the protodog. If so, man's best friend began begging for food scraps about the time that modern humans emerged in Africa—which is highly unlikely, says Klein.

Dating questions aside, once humans succeeded in changing the wicked wolf into loyal Lassie, Wayne says, they apparently quickly developed a "large, ample pool" of dogs to interbreed—and to take with them wherever they went. "That's what this large, well-mixed and worldwide gene pool of dogs suggests," he says. That pattern implies that dogs and people do indeed share an ancient bond, agrees Klein. Besides the dog, only one other mammal has that rare combination of unusual genetic diversity and a widespread, well-mixed gene pool: humans.

–**Virginia Morell**

MEETING BRIEFS

From Clouds to Cores at the Spring Geophysics-Fest

BALTIMORE—When earth scientists gather for the semiannual meetings of the American Geophysical Union (AGU), the fare can range from earthquakes to evolution. This spring, more than 2000 researchers gathered here between 27 and 30 May. They heard diverse presentations that spanned the solar system, from the climate-altering effects of jet contrails in Earth's high atmosphere to the temperatures of the Jovian moons.

Jupiter's Coldhearted Moon

Any parent knows that siblings can be strikingly different, and the same is true in planetary science. Since the spacecraft Galileo began swooping by Jupiter's four largest moons in late 1995, researchers have become increasingly convinced that the three inside moons—Io, Europa, and Ganymede—are geologically complex bodies that even now harbor surprisingly fierce internal fires. But the outermost of the four moons, Callisto, seems to have been left out in the cold, according to the newest Galileo observations reported at the meeting and in a series of recent *Science* and *Nature* papers. Indeed, Callisto may never have warmed enough, even during its early years, to form the internal layering now evident in the other moons. Geologically, Callisto is dead and may never have been fully alive.

JPL/NASA

Family portrait. Jupiter's moons Io, Europa, Ganymede, and Callisto (top to bottom in this composite) have similar sizes but very different life histories.

Now, researchers are trying to explain these dissimilar biographies. Ganymede, for example, may have temporarily occupied an orbit in which Jupiter's gravity kneaded and warmed its interior, a process that is now warming Io and Europa. Callisto, meanwhile, may owe its deathly chill to its formation far from the mother planet's gravitational reach. But the evidence that Callisto was born cold is a puzzle. Because the birth of most moons and planets is thought to be accompanied by plenty of heat, Callisto's undifferentiated interior raises new questions about how such medium-sized bodies form. "The mystery is how you make Callisto this way in the first place," says planetary physicist William McKinnon of Washington University in St. Louis.

The first clue to the vibrant lives of some of these moons came in 1979, when the Voyager spacecraft sent back images of spouting volcanoes on Io. But judging the forces behind a moon's geologic activity can require a look inside, which planetary scientists are now getting from Galileo measurements of the moons' gravity and magnetic fields. A magnetic field like Earth's requires internal heating, usually early in the planet's history, to extract metal from rock and form a molten core, as well as enough lingering heat to keep that core churning to produce a magnetic field. In an overview at AGU, space physicist Margaret Kivelson of the University of California, Los Angeles, explained that the Galileo magnetometer picked up clear signs of internal fields at Io and at Ganymede, and a distinct magnetic signature at Europa that may be a weaker magnetic field. But Callisto clearly generates no magnetic field, meaning that any inner fires it had are now thoroughly damped.

What's more, Galileo's gravity data suggest that Callisto's fires never did flare very high. Such satellites first come together as well-mixed balls of ice and rock, but given enough heat, their constituents will melt and separate into a dense metallic core, a less dense rocky mantle, and a watery shell. Passing spacecraft can detect such layering by detecting subtle variations in a moon's gravitational pull,