

Evolution of the domestic dog

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Introduction

Dogs (*Canis familiaris*) were the first species to be domesticated by humans and are still one of the most important domesticated animals. The partnership between humans and domesticated dogs is based on the help with herding and hunting that dogs provide as well as their companionship and a source of food. Dogs benefit by receiving food, protection and shelter from the relationship. The history of this partnership is however, controversial. This review will present the current evidence to try to address some of these controversies.

Modern dogs, their breeds and their closest relatives

Domestic dogs are members of the genus *Canis* which also contains several other species of wolves, coyotes and jackals. Sometimes any member of the family which they belong to, the Canidae, is referred to as a dog, but here 'dog' will only be used to mean domestic dogs. The relationships between species of the dog family are shown in this diagram (Linblad-Toh *et. al.* 2005). The closest relative of the dog is the grey wolf, *Canis lupus*. This has been confirmed by many other genetic studies (e.g. Wayne 1993).

One complication when looking at the relations of *Canis* is that most of the species in it can interbreed to produce fertile offspring. This is because they all have 78 chromosomes (Vilà, Maldonado & Wayne 1999), apart from two species of jackals found in Africa which have 74. So even if wolves are the closest relatives of dogs, jackals or coyotes could still have contributed to the ancestry. Nevertheless studies on many different genes have always found grey wolves to be much more similar to dogs than coyotes or jackals (Vilà, Maldonado & Wayne 1999).

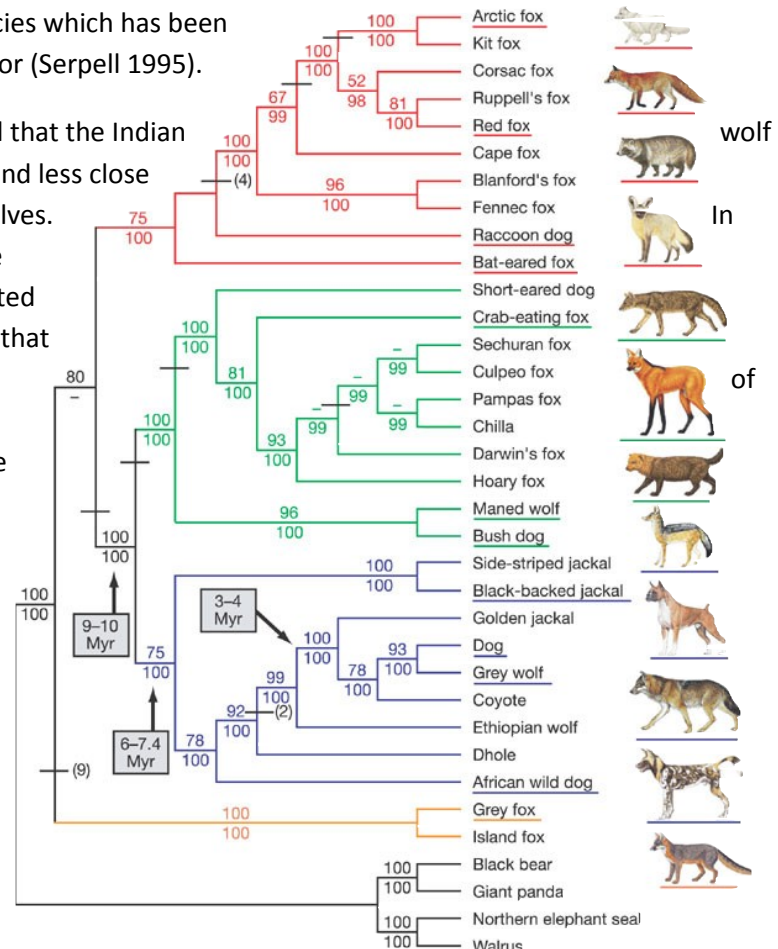
There are also several different types of grey wolf, classified into 37 subspecies. The familiar European and American wolves are examples of the northern sort of wolf, which are larger than the southern subspecies in North Africa, Arabia and India. These southern wolves are smaller, have thinner coats, and tend to bark rather than howl. They would probably be easier to domesticate than the northern subspecies (Hemmer 1990). The picture shows an



example of an Indian wolf, a subspecies which has been named as the most likely dog ancestor (Serpell 1995).

However, genetic studies have found that the Indian is quite distinct from other wolves, and less close genetically to the dog than other wolves. In fact, the differences suggest that the populations could have been separated for 400,000 years ago. This suggests that Indian wolves have not played much a part in dog domestication, which most likely happened only within the last 100,000 years (Sharma, Maldonado, Jhala & Fleischer 2004).

Dogs also have a wide variety of different breeds. It's possible that some of these were domesticated independently; different breeds have certainly interbred and received genes from different types of wolves.



Time and Place of Dog Domestication

The earliest undisputed finds of domesticated dogs are in China at the site of Jiahu in Henan Province, a Neolithic settlement, dated to around 7000 BC. There are many earlier finds which may be of domestic dogs, but are less certain. Several remains of animals which appear intermediate between wolves and dogs have been found in Europe; the oldest is from Belgium's Goyet Cave and dated to 31,700 BC (Germonpré *et. al.* 2008). They show signs such as shorter snouts than wild wolves. But this doesn't mean humans were keeping domestic dogs at that time, only that some wolves were differentiating from others for some reason, which might have nothing to do with domestication (Crockford & Kuzmin 2012). In the burial site of Bonn-Oberkassel in Germany, from 12,000 BC, human and dog bones are found together (Serpell 1995). The dog probably had some kind of significance to humans for this to happen, but it does not necessarily imply domestication. By 6200 BC, a dog skeleton in Siberia, in the Shamanaka site, has been found in a grave buried in a similar way to a human.

The archaeological evidence thus suggests that the dog was domesticated sometime between 35,000 years ago and 10,000 years ago. This is the time when they started to differentiate from wolves. However, there could have been associations between humans and wolves earlier; these dates can only tell us a date by which the dog had been domesticated.

Studies on the Xoloitzcuintli, a native Mexican breed of dog that has been mostly isolated from other breeds, have found that a New World domestication of dogs is unlikely (Vilà, Maldonado & Wayne 1999)—its genes are more similar to Old World breeds than New World wolves. So dogs were

probably not domesticated any later than the last arrival of humans in America before Europeans. Since the Bering land bridge was submerged about 15,000 years ago, it's likely that dogs were domesticated around that time or earlier. Similarly, when the first people came to Australia around 40,000 years ago, they didn't take dogs with them, so dogs were presumably domesticated after that time. The same study found that the Xoloitzcuintli also had a high level of genetic diversity, so there was no bottleneck effect when dogs were brought to the New World; humans must have taken large populations of dogs with them and probably kept bringing in new dogs via continued interaction with the Old World.

The archaeological evidence also suggests somewhere in Eurasia as the place of dog domestication. One study, using mitochondrial DNA, has suggested an origin in East Asia 15,000 years ago (Savolainen *et al.* 2002). Evidence for this comes from the fact that dogs show the greatest genetic variation in East Asia, suggesting they have been introduced into other areas later. However, another study on nuclear DNA in 2010 found the Middle East to be the area with the greatest variation (Bridgett vonHoldt *et al.*). Studies of African dogs have found similar levels of genetic variation there (Anderson 2009). There also the possibility that the dog was domesticated more than once. Certainly there has been a lot of interbreeding between domestic dogs and wild wolves in various areas. So the place of dog domestication is very uncertain.

Lineage of domestic dogs

As explained above wolves are the most genetically similar species to domestic dogs, suggesting that they are the ancestor. However no subspecies of wolf has been established as a particularly close relative of dogs (and therefore a probable ancestor). The most likely candidate based on behaviour and appearance is the Indian wolf, but genetic studies suggest otherwise (Sharma, Maldonado, Jhala & Fleischer 2004).

Koler-Matznick 2002 finds several problems with the origin of dogs from wolves and has instead suggested that the domestic dog may not descend from wolves as we know them, but a closely related species which is now extinct except in domestic form.

One of these problems is the fact that usually, domestic animals tend to go back to their wild form after being feral for many generations, losing most of the differences in appearance and behaviour. This is not what happens, however, with feral dogs. There are many long-established feral populations of dogs around the world, such as dingoes in Australia, which have been feral for thousands of years. The dogs in these feral populations are all fairly similar to each other, but different from wolves, and are known as pariah dogs. As well as Australia they are found in Australia, New Guinea, Southeast Asia, India and southeastern parts of North America. Domestic dogs also hybridise with wild wolf populations only rarely, although it definitely happens—for example, in the endangered population of Italian wolves, there is little evidence of interbreeding with dogs despite their low numbers (Verardi *et al.* 2006). In contrast, Scottish wildcat populations are highly threatened as a distinct population by hybridisation with domestic cats. However, it is the case that domestic dogs are the oldest domestic animal, and have had more time to acquire significant differences from their wild ancestors.

Another problem is that modern wolves are difficult to tame. The fact that wolves live in packs has been seen as making wolves especially suitable for domestication among canids, but unlike species such as cattle living in herds, wolves are capable of living outside the pack and are more independent within it than herd animals. Wild wolves as found today would make poor guards—they will run away from dens containing their own children when faced with danger to themselves—and their hunting strategy of quickly chasing prey would not help humans, who typically need to hunt prey by stealth and ambush (Koler-Matznick 2002). Some aboriginal Australians used dingoes to help them hunt prey, but would only use them to locate prey, and would have to stop them from chasing them away afterwards.

The self-domestication hypothesis

The above evidence argues against the idea of humans taming wolves, but other researchers have suggested that dogs actually evolved by natural selection, from wolves who started to scavenge around human camps. Coppinger 2001 argues that wolves were not actively tamed, but instead populations of them were selected to have a lower flight distance (how close they are willing to get to a dangerous animal, like a human, before running away), gradually creating wolves that were friendly to humans.

This hypothesis is not without problems. Firstly, wolves would have been dangerous to have scavenging around near human sites. In times before the development of long-range weapons, wolves would have been bolder than they are today. Although wolves attack adult humans rarely, they would have been a danger to children as they are still today—in Uttar Pradesh in India from 1996 to 1997, 74 people, mostly children under the age of 10, were killed by wolves (Mech 1998). It's likely that humans would have actively warded wolves away from their camps considering the possibility of these attacks.

It is also not clear that scavenging around human camps would have been a lucrative enough lifestyle for wolves to evolve into before humans became agricultural. Hunter-gatherers typically make as much use of any carcass as possible, leaving little waste (Blumenschine & Marean 1993), and dingoes tamed by Australian Aboriginals are usually in poorer condition, nutritionally, than wild dingoes (Meggitt 1965). If dogs evolved by self-domestication, it seems unlikely that it could have started as long ago as 30,000 years ago, before humans started settling in places for long periods. Given these difficulties, Koler-Matznick 2002 suggests that the hypothesis that dogs were domesticated from a different species or type of canid which was already more suitable for taming is equally likely. She notes that there are some small extinct fossil canids which have usually been classified as subspecies of grey wolves, but they are often found in the same areas as other wolf subspecies. These could be the type of canid that were tamed to give rise to the domestic dog.

The evolution of different breeds

Dogs are distinguished from wolves by morphological traits such as shorter snouts, smaller jaws, teeth, brains and smaller overall size. They also have more of a vertical drop in front of the forehead. Since both dogs and wolves vary considerably, not all of these differences are fairly established; for example Wayne 1986 finds no evidence for shorter snouts in dogs. More firmly established are differences in behaviour—for example wolves only bark when young to attract attention from their

mother, while dogs mainly bark throughout their lives. These traits are found in juvenile wolves, and their retention in adult dogs can be seen as an example of neoteny, where juvenile characteristics are selected to be retained for longer. This selection would have happened because juvenile wolves are more social and less dangerous than adults.

An experiment carried out in Siberia has shown that many of the traits of domestic dogs are not just a coincidence. Researchers took silver foxes (*Vulpes vulpes*), a species which has never been domesticated before, and started a breeding program where they would select the foxes for the single trait of tamability. This research has gone on for more than 50 years—a very short time in evolutionary terms but enough for the artificial selection to take effect. The hypothesis being tested was the idea that changing just this one trait would also bring about changes in lots of other areas which did not seem obviously affected by tamability. The director of the experiment, Dmitry K. Belyaev, had noticed that many domestic animals share common traits such as curly hair, floppy ears, lack of pigmentation in certain areas, and the loss of a seasonal reproductive cycle, which are not commonly found in wild species. By the 10th generation of foxes, some of them had lost pigmentation in parts of their fur. Soon after they gained floppy ears, and by the 15th generation some had shorter tails and legs or underbites or overbites. The seasonal reproductive cycle is still there, but the mating season has lengthened. None of these traits have become common in the whole population of foxes, but the results seem to confirm that that these traits in domestic dogs have arisen as consequences of domestication, with the possible exception of reproduction all year round (Trut 1999).

Looking at the causes of these changes also suggests that they are due to retention of juvenile characteristics, and taking a longer time to mature. For example the lack of pigmentation on parts of the body turns out to be due to the fact that pigment cells initially form in a fox embryo in the same area. They later move to cover the whole skin. But in these foxes, the pigment cells have ended up moving later, which in certain areas leads to them not being able to fully develop into pigment cells and dying.



Of course, not all dogs are the same. Most of the differences between dog breeds can be explained by looking at the purpose of the breed—historically, most dogs have been bred for some kind of work. The first use of dogs would have been to help with hunting. These can be split into sighthounds, which rely on speed and actively catch prey, and scenthounds which detect the presence of prey by following their scent. Naturally sighthounds, like the Saluki in the first picture, have long legs and deep chests holding a large heart, while scenthounds like the beagle below have large drooping ears which are thought to help concentrate scent near the dog's nose, and make loud, deep barks which help humans know where they're going. For agricultural peoples, dogs developed additional uses, such as protecting and herding animals and guarding homes.



Genetic studies have been able to identify several ‘ancient’ breeds of dogs, meaning that they are more basally positioned on phylogenetic trees. Breeds like the Chinese Shar Pei and Chow Chow, the Japanese Akita Inu and the Central African Basenji, the Middle Eastern Saluki, the Afghan Hound, the Alaskan Malamute and the Siberian Husky have been consistently identified as basal breeds (Larson *et. al.* 2012). However, Larson *et. al.* 2012 finds that these basal breeds are not close to the earliest domestic dogs but have

avoided recent interbreeding with other breeds, or in some cases have gone through genetic bottlenecks that have exaggerated their genetic uniqueness. It’s uncertain therefore whether these breeds can be of much use in getting an idea of what early dogs looked like.

There are also many populations of feral dogs which are long-established. There is no reason to think that these are descendants of escaped dogs, rather than descendants of dogs which were only ever partly domesticated. As mentioned above, these tend to have similar characteristics, and some researchers suggest they resemble the ancestral dog population. The images here show a dingo from Fraser Island, Australia on the left and two Carolina Dogs from North America on the right. Dingoes are an interesting case since the first fully domesticated dogs were only brought to Australia by European settlers. Genetic studies seem to indicate that dingoes only arrived in Australia around 5,000 years ago—long after the arrival of aboriginal Australians 40,000 years ago.



Conclusion

Dogs were domesticated from wolves—wolves are closest to dogs genetically and they are capable of breeding with each other to produce fertile offspring, so any dog ancestor would qualify as the same species as wolves. But wolves are not easily tamable. Two possible solutions that have been raised are:

- The hypothesis of Coppinger 2001: wolves were not actually domesticated by humans but domesticated themselves, evolving to live with humans and being accordingly selected for tamability.
- The hypothesis of Koler-Matznick 2001: dogs were tamed from a kind of wolf that was distinct in various aspects which made it easier to tame. It could be seen as a different species, since some other *Canis* species like coyotes are also capable of producing fertile offspring with wolves but are seen as distinct species. In that way it could be said that

domestic dogs are not actually descended from wolves, but it depends how you define your terms.

Where they were domesticated is unclear, but it was probably somewhere in Africa or Asia. Dogs were probably domesticated some time before the development of full agriculture, but identifying an exact date is difficult especially considering that there are different degrees of domestication. There may have been distinctions between domestic dogs and wolves as early as 30,000 years ago.

Belyaev's experiment suggests that the selection of the domestic dog ancestors for their tamability—their lack of aggression and fear towards humans and ease by which they could be tamed—was enough to make them evolve most of their distinct traits, usually by retention of characteristics found in juvenile wolves. Eventually, humans would have started using dogs to help them with tasks like hunting, and after the development of agriculture, herding and guarding homes. Different breeds would probably have started to develop from the start, due to different people having different lifestyles. Feral dogs would also have developed from escaped dogs, or dogs that were just semi-domesticated and given a lot of time to roam freely, and given rise to pariah dogs and dingoes. Dogs spread quickly across all of Africa and Eurasia, and the Americas as well as long as the continents were connected by the Bering land bridge. They were much slower to arrive in Australia, only arriving around 5,000 years ago as wild dogs.

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