

Basenji Origin and Migration: Domestication and Genetic History

by James E. Johannes

Introduction

The Basenji is considered an ancient breed. The history of its origin has been largely speculative. Recent genetic studies and the synthesis of several theories on the development and origin of the dog have thrown more light on the question of the Basenjis' origin.

The Wolf as the Basenji's ancestor

Charles Darwin (1859) thought that the diversity of the dog suggested it originated from two or more wild canine species. Konrad Lorenz suggested that traits from both wolves and jackals could be observed in the dog (Wayne et al., 1999). Green (1959) proposed that the Basenji belonged to the Spitz family and that the Spitz inherited certain jackal characteristics. In Scott's (1968) opinion the possibility that jackals have been crossed with dogs is most likely to have occurred in the African basenji because their vocalizations are different from other breeds. Chromosome number [78] is the same for the dog, jackal, and coyote (Wayne, 1993). Successful breeding between these three canids has occurred.

In the last few years the origin of the dog has been the subject of several studies using genetics. Vila et al. (1997) compared mitochondrial DNA [mtDNA] from 162 wolves and 140 domestic dogs. They concluded that the wolf was the most likely ancestor of dogs. A more recent study by Savolainen et al. (2002a) comparing mtDNA of 654 domestic dogs also suggests that domestic dogs descended from at least 5 female wolf lineages. A limited analysis of mtDNA in 7 dogs and 26 gray wolves found a difference of 0.2%, while the difference between gray wolf and coyote is 4% (Wayne, 1993). A more comprehensive look found divergence between dogs and wolves to be 1.5% in comparison to 7.5% between dogs and coyotes (Wayne et al., 1999). No dog sequence differed from any wolf sequence by more than 12 substitutions, whereas dogs differed from coyotes and jackals by at least 20 substitutions and two insertions. More limited studies of nuclear markers also support the conclusion that the wolf was the ancestor of the domestic dog (Vila et al., 1997).

Mitochondrial DNA is limited to the maternal side of genetic inheritance. If the jackal is part of the Basenjis' makeup, then it is more likely that rare matings between female Basenjis and male jackals would have occurred. This would not show up in the mtDNA. Physical evidence also rules out the jackal from the ancestry of the Basenji. The jackal has a smaller brain than a dog of comparable size (Epstein, 1971). Most domestic animals have become smaller as compared to their wild progenitors (Tchernov et al., 1991). Brain size was also reduced (Rohr et al., 1999). Two basic cranial trends occur both in the wolf and dog [i.e. decumanides and veltrides] but were not present in the jackal (Epstein, 1971). The teeth and cranium, for the most part, are true to the wolf type in the dog. Every domestic dog has the specialized first upper molar with reduced cingulum of the wolf, and not the primitive jackal tooth (Epstein, 1971).

Point of Origin

For years many people have speculated on several questions on origin of the dog. Where did the dog first become domesticated, when did it happen, and what wolf species was the progenitor?

Archaeological evidence seemed to point to South West Asia as the area of origin for the dog. Dogs 12,000 years old were identified in Israel as perhaps the oldest domestic dog remains found (Davis et al., 1978). Others thought the dog arose from different subspecies of wolves at several places in Europe, India, North America, and China, thus explaining the diversity of breeds (Morey, 1994).

Savolainen et al. (2002a) suggested that dogs originated in East Asia. The number of shared and unique mtDNA haplotypes was highest for East Asia. The date of origin was estimated to be approximately 15,000 to 40,000 years before present.

Most domestic dogs have a morphological feature in the mandible that is diagnostic in differentiating dogs from wild canids. The apex of the coronoid process [see Figure 1] of the ascending ramus is turned back toward the posterior (Olsen et al., 1977). This feature is also present in the Chinese wolves [*Canis lupus chanco*] and in the Indian wolf [*Canis lupus pallipes*] (Koler-Matznick, 2002). It is possible that either of these wolves is the ancestor of the dog.

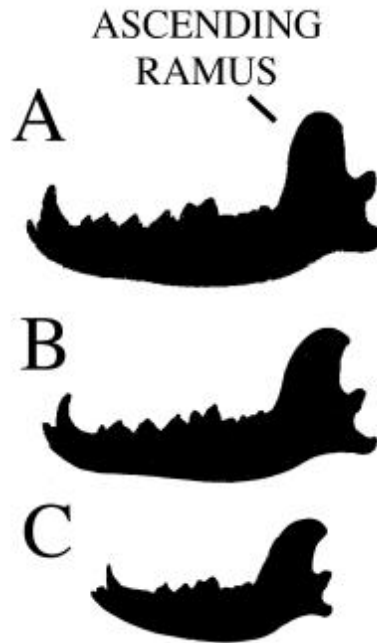


FIGURE 1 - Outline of the mandible for the [A] North American wolf, [B] Chinese wolf, [C] and domestic dog.

Self domestication

The process of domestication has long been assumed to be a conscious undertaking by ancient man. The favored scenario postulate that a population of wolves was intentionally isolated from wild wolves by taking wolf puppies and raising them. From this population the domestic dog arose (Coppinger et al., 2001). This hypothesis recently has come into question.

Wolf and dog puppies develop at the same rate and are dependent for milk at nineteen days. Wolf puppies not socialized to humans before nineteen days will never accept humans, while dog puppies can still be socialized to humans at ten weeks of age (Coppinger et al., 2001). The window of opportunity for socializing a wolf puppy is smaller than that of dogs. Wolves that are not afraid of humans are more dangerous than a wild wolf. Wolves will test their human masters repeatedly for dominance. The prey drive is higher than in a dog. Small children are at risk of being viewed as prey when they run and scream while playing. Ancient people also had no fences, so when the wolf puppy developed into an adult it would most likely run off to find a mate in the wild (Coppinger et al., 2001). The process of domestication would have to start again with a new puppy.

Speciation requires populations that evolve, not individuals (Coppinger et al., 2001). Speciation can occur when a segment of a species population is isolated (Darwin, 1859). It is now believed that wolves domesticated themselves. As man settled into more permanent homes, after the Ice Age, a new habitat was created where leftover food was available in a small area. Acquiring this food was easier than hunting, but most wild wolves will run away from humans on sight. Wolves more fearful of humans ran away and did not come back for a long period or not at all. Wolves that were less afraid came back earlier or did not run far and were able to take better advantage of the food available in the new habitat. In the human impacted area natural selection favored wolves less fearful of humans [see Figure 2]. This new population of less fearful wolves started living permanently in the human impacted area and became separate from wild wolves. This separation allowed for the development of the dog.

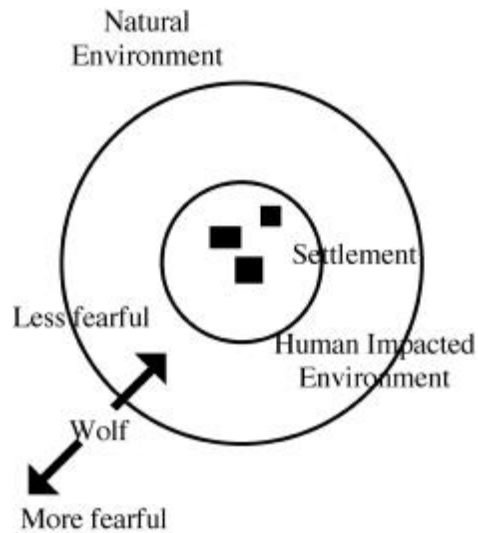


FIGURE 2 - New habitat zone created by human settlement separated less fearful wolves from fearful wolves.

Evolving into dogs

The dog is different from the wolf both physically and behaviorally. How did this change happen so quickly? Ongoing research in Siberia may have the answer.

In 1959 Dr. Dmitry Belyaev began an experiment to answer the question if the observed changes in the dog from the wolf could be a result of selection for single behavioral trait, in this case fearfulness. He believed that the behavioral responses are regulated by fine balance between neurotransmitters and hormones at the level of the whole organism. The genes that control that balance occupy a high level in the hierarchical system of the genome. Even slight alterations in those regulatory genes can give rise to a wide network of changes in the developmental processes they govern. Selecting for behavior possibly could cause far-reaching changes in the animals' development.

He chose the silver fox as his test subject. For sixty years the fox had been raised for fur on farms in Russia, but retained their fear of man. Belyaev started with 30 male foxes and 100 vixens obtained from a fur farm in Estonia. The offspring were evaluated and selected on tameness alone. Selection was strict, with not more than 4 or 5 percent of male offspring and 20 percent female selected to breed. Each generation was tested for tameness. The foxes were graded into several classes. Class III foxes flee or bite if stroked or handled. Class II let themselves be petted but showed no friendliness. Class I are friendly, often wagging their tails and whining. The highest class was IE [domesticated elite]. This class of foxes was eager to establish human contact, whimpering to attract attention and sniffing and licking experimenters like dogs. By the tenth generation 18 percent of the foxes were in this class; by the fortieth generation 70 to 80 percent of the population fell in this class (Trut, 1999). Other behavioral changes occurred. The critical period of socialization increased from 40-45 days in unselected foxes to 60-65 days in the selected foxes (Belyaev et al., 1984/1985). In moments of emotional excitement, domesticated foxes even sound like dogs (Belyaev, 1979).

Not only did domestication change behavior, morphology also changed. The domesticated foxes began to develop piebald coats and a star pattern [blaze] on the forehead. Floppy ears, shortened legs and tails, tails curled upward like dogs, and underbites and overbites also began to show up. Changes in the skull, cranial height and width tended to reduce; and snouts tended to be shorter and wider than those of a control group of farmed foxes. Foxes are normally strict seasonal breeders; but changes also occurred in the annual cycle of some of the domesticated foxes. For instance, some reached sexual maturity a month early, had larger litters [one more pup on average], breed out of season, and a few mated twice a year (Trut, 1999).

The Fox Farm experiment suggests that a change in the level of fearfulness has a large impact on behavior and morphology and provides a possible explanation on how wolves evolved into dogs.

Genetic History of the Basenji

The Basenji was included in two genetic studies that sought to find the origin of the dog. Both studies used mitochondrial DNA.

The first study by Vila et al. (1997) showed that within breeds, the mtDNA sequence diversity is high. Mitochondrial haplotype diversity could not be partitioned according to breeds and breeds shared sequences with other breeds. For example, the Basenji [1 sampled] shared sequences with the Chinese Crested, Chow Chow and Tibetan terrier (Vila et al., 1997). Moreover, dog sequences cluster with different groupings of wolf haplotypes suggesting dogs and wolves may have continued to exchange genes after the dog arose from the wolf

In the second study by Savaolainen et al. (2002a) a phylogenetic analysis of the data assigned the dog sequences into five clades (A, B, C, D, and E). Eleven Basenjis were included in this study, and their sequences all fell within

clade A. In the Basenjis sampled three different haplotypes were found. This study also included 38 Eurasian wolves. Three wolf haplotypes found in China and Mongolia were contained in clade A. Two of the Basenjis' haplotypes are unique to the west [defined as areas west or east of a line running from the Himalayas to the Ural Mountains] and one was shared between east and west. Of the two western haplotypes, one is unique to the Basenji. The data in the study indicated that haplotypes of clade A in the western part of the world originate from the introduction of a subset of East Asian types, from which the types unique to the west have later developed (Savolainen et al., 2002a).

Shared sequences for the Basenji with other breeds was also shown in the study by Savaolainen et al. (2002a) [see Figure 3]. The Basenji shares sequences with dogs from East Asia, Siberia, South West Asia, Africa, but not from Europe, India, South East Asia or Arctic America. In the second column of Figure 3 some unexpected breeds are closely related to the Basenji, such as the Tibetan terrier and Siberian Laikas.

The last column in Figure 3 lists the breeds and dogs that are more distantly related to the Basenji. Some breeds have very similar morphology to the Basenji, such as the Singing Dog, Caanan Dog, or Shiba Inu. Others listed in the third column have very different morphology from the Basenji, such as the Pekingese or Border terrier. The results suggest that the majority of breeds, including the Basenji, are genetically diverse and are not well differentiated.

The oldest haplotype originating in East Asia for the Basenji is A5 (Savolainen et al., 2002b). Dogs with this haplotype went east into Japan (indicated by the Ryukyu), north into Siberia (Laika), and west into Tibet. Two areas show no incidence of this haplotype, India and South West Asia. It is possible that it does not occur in India, but it most likely occurs in the dogs of South West Asia since it occurs in dogs of Africa. The absence of haplotype A5 from India suggests that the Basenjis' ancestors only took a northerly route around the Himalayan Mountains. This could change with more research; it is possible the Basenji had ancestors that also took a southerly route.

In South West Asia a new haplotype A9 arose that this study showed only existed in the Basenji and Saluki (Savolainen et al., 2002b). This indicates both could have a common ancestor. Once in central Africa, the Basenji was isolated, and a haplotype [A32] unique to the Basenji probably came about.

Region	Breeds having at least one identical haplotype to the Basenji [A5, A9, A32]	Breeds or dogs [location given] having a haplotype with one mutational step from the Basenji
Arctic America		Alaskan Husky, Alaskan Malamute, Greenland dog.
South East Asia - Thailand, Indonesia, New Guinea		[Indonesia], [Thailand], Thai ridgeback, Singing Dog
Siberia	East Siberian Laika [A5], West Siberian Laika [A5].	East Siberian Laika, Siberian Husky.
East Asia - China, Tibet, Korea, & Japan	Tibetan terrier [A5], Ryukyu [A5], *Chow-chow, *Chinese-crested.	Akita, Chow-chow, [Guangxi], Hokkaido, Jindo, Kai, Kishu, [Laioning], Mikawa, Mops, Pekingese, Pugsan, [Shanxi], Shar-pei, Shiba, Shikoku, [Sichuan], [Tibet].
India		[unknown]
South West Asia – Iran, Turkey, Israel, Saudi Arabia, Syria, Afghanistan	Saluki [A9].	Akbasch, Anatolian pariah, Anatolian shepherd, Caanan, Greyhound, [Iran], Kangal, Kaukazkaia Outjarka, Saluki, Taigan.
Africa	Sloughi [A5].	Nguni, Rhodesian ridgeback, Sloughi.
Europe		Basset griffon, Border terrier, Buhund, Cavalier King Charles spaniel, Chesapeake Bay retriever, Drever, Finnish lapphund, Finnish spitz, Flatcoated retriever, Fox terrier, German Shepard, Golden retriever, Gos d'atura Catalan, Icelandic sheepdog, Irish Setter, Kerry blue terrier, Leonberger, Mudi, Newfoundland sheepdog, Norfolk terrier, Norrbottenspets, Norwegian elkhound, Pointer, Papillon, Pug, Pyreneean mastiff, Rottweiler, Vastgotaspets, West highland terrier, Whippet.

FIGURE 3 – Breeds or dogs with mtDNA haplotypes that are identical or one mutational step from the Basenji shown by region. Source: Savolainen et al., 2002b; *Vila et al., 1997.

Conclusion

Genetic and physical evidence support the wolf as being the ancestor of the Basenji. The creation of a new habitat by the settlement of man caused the separation of fearful wolves from less fearful wolves. The gradual reduction of fear toward man precipitated changes both behavioral and physical in the wolf that finally brought about the development of the dog. The Basenjis' ancestor came out of East Asia and migrated west to Africa.

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Glossary

- chromosome* - n.: a threadlike body in the cell nucleus that carries the genes in a linear order.
- cingulum* - n.: [anatomy] an encircling girdle-like structure [as the ridge around the base of a tooth].
- decumanides* - [brachygnathic platycephalic decumanides] cranial type characterized by a broad skull, short frontals and maxillae and long parietals, as represented by the Great Dane.
- haplotype* - The set, made up of one allele of each gene, comprising the genotype.
- mitochondrial* - adj.: referring to mitochondria [a small intracellular organelle which is responsible for energy production and cellular respiration].
- veltrides* - [dolichognathic leptycephalic veltrides] cranial type characterized by a narrow skull, long frontals and maxillae and short parietals, as represented by the German Shepherd dog.