

## Controversies of Origin of Domestic Dog - III - References of Modern Dogs until 2006

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### Review Article

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**Abstract:** The domesticated dog was used not only to protect properties and warn of approaching animals or humans by barking day or night, but also it was used to hunt and even as pet as a man's close friend for centuries. The origin of dog always has been a controversial issue. The majority of the scientists from Belgium, Canada, Finland, France, Germany, Portugal, Russia and USA claimed that domestication happened in Europe but domestication time was not definite. Also some scientists from China, Sweden and USA claimed that the domestication happened in Southeast of Asia. At last one scientist from Israel claimed that possible origin of dog was Middle East. Altogether there is still no definite answer about place and time of domestication.

**Keywords:** *Canis familiaris*, *c. lupus*, Domestication, wolf, DNA analysis

### INTRODUCTION

The genus of *Canis* contains eight extant species including gray wolf (*Canis lupus*), red wolf (*C. rufus*), coyote (*C. latrans*), golden jackal (*C. aureus*), striped jackal (*C. adustus*), black-backed jackal (*C. mesomelas*), Ethiopian wolf (*C. simensis*), and domestic dog (*C. familiaris*). The domestic dogs live in all countries except Antarctic because of international ban. IN the world there are also some feral dog population including the Dingo (*C. f. dingo*) of Australia and the New Guinea Singing dog (*C. f. hallstromi*) which are apparently extinct in the wild [1]. The domestic dog is phenotypically one of the most variable mammal species [2, 3] like horses and pigeons [4, 5]. The origins of the dog always have been debated among scientists [6-9]. It is quite understandable because there are more than 400 various breeds which range from tiny Chihuahuas to huge Saint Bernard [10]. Under intensity of human-animal relationship, three various pathways were offered as commensal, prey and directed domestication. Dog was accepted as a directed domesticated species together with cat, rat, mouse, guinea pig, chicken, pigeon, duck, turkey and possible pig [11].

Even though all scientists agree with that the dog was domesticated from wolf, the geographic origin and time of dog is uncertain. The purpose of this study is to review origin of dogs regarding with genetic relationship to other dog breeds and canids. Fossil dog bones which were unearthed from ancient archaeological sites were ignored in this review. Fossil dog bones and ancient dogs are going to be reviewed in another paper.

### The Beginning Studies (Until 1990)

Simonsen was one the first researcher of *Canidea* genetics about dog domestication by using electrophoresic studies. She analyzed blood samples of dog, wolf, coyote, jackal, Hallstrom (New Guinea Singing) dog, dog-wolf hybrid, and dog-jackal hybrid. In the study zymograms of 18 enzymes and 3 proteins were investigated. According to results 14 enzymes and

1 protein had identical zymograms both in dogs and wolves [12]. A study was realized to search interrelationships of chromosome banding patterns in canids, mustelids, hyena, and felids. The results showed that all canids were karyotypically very similar to one another [13]. Researches proved that DNA fingerprints of cats and dogs could prove suitable for individual identification and for establishing family relationships. They were also suitable for rapid marker generation in large pedigrees and could be applied to linkage analysis in these animals [14]. Allozyme divergence was studied among *Canidea* family by using blood and tissue samples 12 of 14 extant canid genera. It could be said that African wild dog (*Lycan pictus*) and Coyote (*Canis latrans*) separated from the line of Grey wolf (*Canis lupus*) and Domestic dog (*Canis familiaris*) approximately 3 million years before present [15]. Modi *et al.* [16] carried out a research to investigate

chromosomal localization of satellite DNA sequences among 22 species of felids and 10 species of canids. They found that about 90% of all grains were located at autosomal centromeres, and grains were absent from the sex chromosomes among the canids. The same year Fanning *et al.* [17] published an article about evolution of heterochromatin-associated satellite DNA loci in felids and canids. The results demonstrated that the satellite families within the canids were showed to be more uniform in regard to both amount/sequence and restriction patterns, although some canid species did differ significantly from the consensus in both respects. Another study was carried out by Fanning to survey about molecular evolution of centromere-associated nucleotide sequences in two species of canids. According to observed results the sequence data from 16 monomers of dog satellite and 19 monomers of grey fox satellite demonstrated that the substitution spectra were different in the two canid species [18].

#### **The Japanese Researchers (1991-1995)**

Tanabe conducted a study by using blood proteins and enzymes to find polymorphisms. He included 3.632 dogs including 46 of Eskimo, Korean, Chinese, Russian, Bangladesh and Japanese breeds. They observed genetic variations in six loci composed of seven non-enzymatic proteins and nine enzymatic proteins. The results showed that there were two gene flows in dogs into Japan. The first gene flow was from Southeast Asia through the Ryukyu Island to all the Japan Islands. The second gene flow was from Korean Peninsula. There was none of gene flow from Russia even though it is near to Japanese Islands [19].

In order to calculate a genetic relationship among dog breeds, various methods used to be used. For example first qualitative data were calculated and they were transformed and introduced in to form of a matrix distances by using Sneath and Sokal Method [20, 21]. The gray wolf has a vast geographic range included most of the Northern Hemisphere. The mitochondrial DNA (mtDNA) variability among 26 populations of wolves from throughout their geographic range was investigated. The 18 mtDNA genotypes in gray wolves were found and seven of 18 were derived from hybridization with coyotes, four of 18 were limited to the New World, and six of 18 were limited to the Old World and the last one was shared by both areas [22]. A short interspersed nucleotide (nt) element (SINE) which was a highly repetitive DNA sequence possibly unique to canids was cloned from the genomic DNA of the domestic dog. Southern-blot analysis of canine DNA indicated that the SINE was widely dispersed throughout the genome. Hybridizations also indicated that the element may be unique to canids and is absent in a variety of other mammals, including members of four closely-related carnivore families [23].

A research was implemented to clarify the identification and characterization of dinucleotide

repeat (CA)<sub>n</sub> markers for genetic mapping in dog. After analysis a large block of simple sequence repeat (SSR) polymorphisms for the dog genome had been isolated and characterized [24]. The same year Holmes *et al.* carried out a study to succeed isolation and characterization of microsatellites from domesticated dogs. They had been isolated microsatellite sequences comprising (dC-dA)<sub>n</sub>(dG-dT)<sub>n</sub> repeats from domesticated dogs libraries and sequenced [25].

According to scientists the most endangered canid of the world is the Ethiopian wolf (*Canis simensis*). It is lived in six isolated areas of the Ethiopian highlands with a total population of no more than 500 individuals. The molecular techniques used proved that the Ethiopian wolf was a distinct species more closely related to gray wolves and coyotes than to any African canid. Hence an immediate captive breeding program of Ethiopian wolves should be applied to protect their gene pool from dilution and further loss of genetic variability [26]. Rothuizen *et al.* [27] conducted a study to calculate the incidence of mini and micro-satellite repetitive DNA in the canine genome. He observed that the di-, tri- and tetra-nucleotide short tandem repeats, as well as some minisatellite sequences, were potentially useful as genetic markers, for mapping of the canine genome, and also for paternity testing and the analysis of population characteristics. A group of scientists actualized an analysis to find a pattern of genetic differentiation by distance to exist among wolflike canid populations in North America. According to results wolves and coyotes did not show a pattern of genetic differentiation by distance. Although the genetic subdivision in coyotes was not significantly different from zero, gray wolves showed significant subdivision [28].

In 1995 one hundred and one new dinucleotide repeat polymorphisms specific for the canine genome had been identified and characterized. Over 200 of clones were sequenced and 101 polymorphic markers were defined. 54 markers were found to be highly or very highly polymorphic as they had four or more alleles when tested on a panel of unrelated dogs. This group of markers could be useful for following inheritance of traits in crosses between dogs [29]. In a case study a frequency distribution and allele size in 20 canine microsatellite loci were analyzed by using 33 flat-coated retrievers, 32 dachshunds, 10 red foxes, and 10 Arctic foxes. 80% (16 of 20) of the canine microsatellite primer pairs amplified corresponding loci in the two fox species. This reflected a very high sequence conservation within the Canidae family relative to findings in that possible indicated to utilize the well-characterized fox karyotype instead of the dog karyotype [30]. Holmes *et al.* [31] made research for 18 microsatellites in dogs. The Mendelian inheritance of each microsatellite was verified by using families of

Irish setters and Miniature long-haired dachshunds. The observed results proved that the segregation of the alleles did not deviate from the expected pattern.

#### Studies from three Continents (1996-2000)

DNA analysis works were performed by some Japanese scientists in middle of 1990s. One of the first study was performed by Okumura *et al.* [32] to estimate intra and interbreed genetic variations of mitochondrial DNA major non-coding regions in Japanese native dog breeds. They used 73 dogs of eight Japanese native breeds and 21 dogs of 16 non-Japanese dog breeds to calculate polymerase chain reaction and their DNA sequences. According to observed results they classified the dogs into four various groups for phylogenetic analysis. The deepest branchpoint of those dogs phylogeny was calculated about 100.000 years ago. The same year Langford *et al.* [33] fished some results by using peripheral blood lymphocyte cultures and dual-laser flow cytometry. According to observed data high-resolution bivariate flow karyotypes of the dog in which 32 peaks are resolved. Wiczorek [34] carried out a study in 215 white coated shepherd dogs including breeds of Polish Tatra, Slovakian Chuvach, Hungarian Kuvasz, Italian Maremma, French Pyrenean and Turkish Akbash Shepherd dogs. According to observed results Hungarian kuvasz is the most different breed from all examined. The results also showed that the smallest genetic distance is between Slowensky Chuvach and Pyrenean Mountain dog and between Akbash dog and Polish Tatra sheepdog.

Another group of scientists performed a study to determine a class of highly polymorphic tetranucleotide repeats for canine genetic mapping. They realized and characterized a new class of polymorphic markers for the canine genome from a simple tetranucleotide repeat sequence, (GAAA)*n* [35]. Reimann *et al.* [36] tried to demonstrate an extended nomenclature of the canine karyotype by using X and the Y chromosomes. An ideogram of the canine karyotype with 460 numbered bands and characteristic landmarks was identified after analysis. Like Reimann research another research was implemented for standardization of the G-banded canine (*Canis familiaris*) karyotype. In this study 22 of the 39 G-banded chromosome pairs and their corresponding ideograms contained altogether 235 bands had been standardized [37]. The Mexican wolf (*Canis lupus baileyi*) is an endangered subspecies of gray wolf. Garcia-Moreno *et al.* [38] compared with 4 captive population of Mexican wolves to 42 domestic dogs, 151 northern gray wolves and 142 coyotes to define whether uncertified Mexican wolves had specific markers from those animals. The captive populations were genetically more identical to each other than to any other population of dog or wolf-like canid.

After one year another a group of Japanese scientist realized a study to investigate origin of dog by using D-loop region of mitochondrial DNA polymorphisms. They compared with 34 dogs of 24 breeds belonged to Japanese and non-Japanese breeds to 3 subspecies of gray wolf (*Canis lupus lupus*, *C. l. pallipes*, *C. l. chanco*). The results showed that there were a close relationship between domestic dogs and wolves [39]. The same year, in 1997, at Wayne Laboratory a mtDNA analysis study was performed by Vila and with his colleagues [40]. Vila *et al.* used 140 dogs representing 67 breeds and five crossbreeds and 162 wolves representing 27 populations from throughout Europe, Asia and North America. He also used five coyotes (*Canis latrans*), two golden jackals (*C. aureus*), two blackbacked jackals (*C. mesomelas*) and eight Simien jackals (*C. simensis*). They also were potential ancestors of the domestic dog, because all wild species of the genus *Canis* can interbreed [41]. After one year the research of Garcia-Moreno *et al.* [38], Hendrick *et al.* [42] accomplished an analysis for three captive Mexican wolf lineages named as Certified, Ghost Ranch and Aragon lineages. The results proved that all of the lineages consisted of Mexican wolves, and none of them appeared to have ancestry from dogs or coyotes. On the other hand the Certified lineage had the lowest level of inbreeding and had retained the most founder alleles, whereas the Ghost Ranch had a high level of inbreeding and fewest founder alleles by based on pedigree analysis.

The same year Vila *et al.* [40] performed another study. They performed the DNA analysis among the genus *Canis* found 26 dog and 27 wolf haplotypes. Four of 27 wolf haplotypes, W2, W7, W14, and W22, had a widespread distribution. They realized that only haplotypes D6 also observed in some gray wolves from western Russia and Romania. After a phylogenetic analysis there were four monophyletic clades. The Clade I contained 19 of the 26 dog haplotypes which represented many common breeds such as Dingo, New Guinea Singing Dog, African Basenji and Greyhound. The Clade II comprised dog haplotype D8 which belonged to Scandinavian breeds of Elkhound and Jämthund and closely related to two wolf haplotypes from Italy, France, Greece, and Romania. The Clade III covered three dog haplotypes of D7, D19, and D21 which observed in breeds of German Shepherd, Siberian Husky and Mexican Hairless. The Clade IV included three haplotypes of D6, D10, and D24 which were identical to a wolf haplotype W6 found in Romania and western Russia which suggested recent hybridization between dogs and wolves. The variability of 19 canine microsatellite loci was examined within and between three pure breeds of dog including breeds of Greyhounds, Labradors, and German Shepherds. According to observed results none of the three pure dog breeds corresponds to Hardy-Weinberg equilibrium. The results also proved that

pairwise genetic distances of Greyhounds and German Shepherds had longer diverse evolutionary histories than Greyhounds and Labradors or Labradors and German Shepherds [43].

In 1999 Wayne and Ostrander [44] claimed that a phylogenetic comparison of mitochondrial DNA sequences in dogs and gray wolves showed that dogs might have originated from multiple wolf populations at a time much earlier than suggested by the archaeological record. Wayne and Ostrander suggested that the dogs could be domesticated over 100,000 years ago. In the same year Vila *et al.* [2, 45] alleged that dogs could be originated from or interbred with wolves throughout their history at different times and places. Even the breed of Xoloitzcuintli which has been kept isolated for thousands of years could be one of the domesticated breed in North America. In additional Xoloitzcuintli dog had a high level of mtDNA sequence variation. Vila and Wayne [2, 45] also claimed that European populations of gray wolves had extensively hybridized with domestic dogs. Neff *et al.* [46] discussed the utility of the current genetic linkage map and summarized steps necessary for future genetic linkage map improvement. Zajc and Sampson [47] designed a research to investigate canine microsatellites by using blood samples of 53 Greyhound, 52 Labrador and 53 German Shepherd dogs. As a result Greyhounds expressed significantly lower polymorphism than the other two breeds.

#### **Dominance of Scandinavian Researchers (2001-2005)**

A study was applied to analyse genetic variability at four microsatellite loci on the canine Y chromosome in Scandinavian wolves. In the study also haplotypes were calculated together with these four microsatellites. The observed data were used to study the genetic status of the Scandinavian wolf population which contained 60–70 animals in that year but was thought to have been extinct in the 1970s. Research team also analyzed a sample of 100 male wolves from northern Europe and they found 17 different Y chromosome haplotypes among them. Only two of those were found in the current Scandinavian population. This indicated that there should have been at least two males involved in the founding of the Scandinavian wolf population after the bottleneck in the 1970s. The two Scandinavian Y chromosome haplotypes were not found elsewhere in northern Europe, which indicated low male gene flow between Scandinavia and the neighbouring countries [48].

Savolainen was involved in a project by Chinese researchers to investigate East Asian origin of domestic dogs. The team examined the mitochondrial DNA (mtDNA) sequence variation among 654 domestic dogs representing all major dog populations worldwide. The observed data indicated that >95% of

all sequences belonged to three phylogenetic groups. It implied that there was a common origin from a single gene pool for all dog populations. It was also observed that a larger genetic variation in East Asia than in other regions and the pattern of phylogeographic variation suggested an East Asian origin for the domestic dog about 15,000 years ago [49]. Sometimes crossbreeding between wolves and dogs in the wild had been reported, but always poorly documented in scientific literature. A study demonstrated the results of molecular genetic analyses of 31 wolf samples collected in Latvia from 1997 to 1999, including six pups originated from a litter found in northern Latvia in March 1999, and six wolves showing morphological traits that suggested hybrid origin. Nucleotide sequencing of the hypervariable part of the mtDNA control-region and genotyping of 16 microsatellite loci proved that both pups and the morphologically anomalous wolves might originate from crossbreeding with dogs [50]. Another research was achieved for European wolves by comparing with dogs. The relatively large number of class II alleles existed in both European and North American wolves confirmed to their large historical population sizes, yet there were few alleles shared between these regions at DQB and DRB1. The results also showed that the dog had an extensive array of class II MHC alleles, a consequence of a genetically diverse origin, but allelic overlap with wolves only at DQA [51].

Adams *et al.* [52] carried out sequence analysis of the mitochondrial DNA control region from 112 southeastern US coyotes (*Canis latrans*) revealed 12 individuals with a haplotype closely related to those in domestic dogs. The results proved that phylogenetic analyses grouped this new haplotype in the dog/grey wolf (*Canis familiaris*/*Canis lupus*) clade with 98% bootstrap support. Those results showed that a male coyote hybridized with a female dog, and female hybrid offspring successfully integrated into the coyote population. Koskinen [53] applied an investigation to detect the efficiency of the clustering methods in identifying the breeds of origin of 250 domestic dog (*Canis familiaris*) individuals based on 10 microsatellite loci. According to the results an  $F_{ST}$  of 0.18, mean expected gene diversity of 0.6 across 10 loci, and approximately 50 individuals per reference population suffice to provide maximum individual assignment success in *C. familiaris*. This rejected the traditional view that DNA based dog breed identification was not feasible at the individual level of resolution.

A research team materialized a study to analyze the genetic variation in 28 dog breed populations with 100 microsatellite markers. One hundred autosomal microsatellite markers distributed across the canine genome were used to examine variation within breeds. Resulting breed-specific allele frequencies were then used in an attempt to elucidate phylogeny and genetic distances between breeds.

Although the set of autosomal microsatellites was useful in describing genetic variation within breeds, establishing the genetic relatedness between breeds was less conclusive. A more accurate determination of breed phylogeny would likely require the use of single-nucleotide polymorphisms [54].

A research team compared the gene expression patterns in dogs, wolves and a close relative, the coyote, in three parts of the brain: hypothalamus, amygdala and frontal cortex by using microarray technology. They also identified genes with region-specific expression patterns in all three species. The study demonstrated that rapid changes in brain gene expression might not be exclusive to the development of human brains. Instead, they might provide a common mechanism for rapid adaptive changes during speciation, particularly in cases that present strong selective pressures on behavioural characters [55]. The same year Parker *et al.* [56] accomplished molecular markers to study genetic relationships in a diverse collection of 85 domestic dog breeds. Differences among breeds accounted for about 30% of genetic variation. Microsatellite genotypes were used to correctly assign 99% of individual dogs to breeds. Phylogenetic analysis separated several breeds with ancient origins from the remaining breeds with modern European origins. The team also identified four genetic clusters, which predominantly contained breeds with similar geographic origin, morphology, or role in human activities.

A research was carried out to define the origin and time of arrival to Australia of the dingo. In the study 582 bp of the mtDNA control region were analyzed in 211 Australian dingoes sampled in all states of Australia, 676 dogs from all continents, and 38 Eurasian wolves, and 263 bp were analyzed in 19 pre-European archaeological dog samples from Polynesia. The research team also found a mean genetic distance to A29 among the dingo mtDNA sequences indicates an origin about 5,000 years ago. Those results gave a detailed scenario of the origin and history of the dingo that dingoes had an origin from domesticated dogs coming from East Asia, possibly in connection with the Austronesian expansion into Island Southeast Asia [57].

In 2005 there were four studies carried out from various places of the World. Bali street dogs were investigated for genetic variation by using microsatellites in Indonesia. 31 polymorphic microsatellites were analyzed for 40 dogs by comparing Australian dingoes and 28 American Kennel Club breeds. The results showed that the Bali street dog to be highly heterogeneous and related to populations of East Asian origin. These results proved that a viable and diverse population of dogs existed on the island of Bali prior to its geographic isolation approximately 12,000 years ago. Those dogs also had been little influenced by domesticated European dogs since that time [58]. Berryere *et al.* achieved a study to search about dog

coat colour genetics regarding Agouti allele with fawn or sable coat colour in domestic dogs. The study contained 37 breeds, by identifying an Agouti allele with two missense alterations. Agouti alleles of A82S and R83H were present in 41 dogs (22 breeds) with a fawn or sable coat, but were absent from 16 dogs (8 breeds) with a black-and-tan or tricolour phenotype. As a result this work resolved some of the complexity in dog coat colour genetics and provided diagnostic opportunities and practical guidelines for breeders [59].

van Asch and her team realized an experiment to fish 143 of four Portuguese native dog breeds analyzing mtDNA. According to results 15 haplotypes belonging to four major haplogroups were found in these breeds, of which five are newly reported. The team also commented on four subjects about mtDNA haplotypes in dogs across the world. First breeds tended to display haplotypes belonging to different haplogroups. Secondly haplogroup A was present in all breeds, and even uncommon haplogroups were highly dispersed among breeds and continental areas. Thirdly haplotype sharing between breeds of the same region was lower than between breeds of different regions. Fourthly the genetic distances between breeds did not correlate with geography [60]. Lindblad-Toh *et al.* [61] executed an experiment with a crowded team to detect genome sequence, comparative analysis and haplotype structure of the domestic dogs. The team notified a high-quality draft genome sequence of the domestic dog, together with a dense map of single nucleotide polymorphisms across breeds. Analysis of SNPs revealed long-range haplotypes across the entire dog genome, and defines the nature of genetic diversity within and across breeds. The current SNP map now showed it possible for genome-wide association studies to identify genes responsible for diseases and traits, with important consequences for human and companion animal health [61].

## CONCLUSION

What was the purpose of the domestication? Food, hunting, guarding or companionship? How many times the domestication happened? One time or multiple times? Where the domestication happened? In China, Europe, Eurasia, or Middle East? When the domestication happened? 12.000 or 500.000 years ago? Despite many theories there was a general indisputable opinion of the origin of the domestic dog that they were all descendants of the wolf, in spite of the huge variation in size and shape for the lashings of dog breeds. At last it can be concluded that there are still many challenges about processes of dog domestication.

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