

Controversies of Origin of Domestic Dog - IV - References of Modern Dogs after 2006

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Review Article

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Article History

Received: 10.11.2017

Accepted: 18.11.2017

Published: 30.11.2017

DOI:

10.36347/sjavs.2017.v04i11.009



Abstract: Generally the domesticated dog is accepted as a very symbolic example among the domesticated species. 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. There is no doubt about ancestor of dog which is wolf, but there are always arguments about time and place of domestication. There are three different place of domestication including Europe, Southeast of Asia and Middle East, but domestication time was not definite. Altogether there is still no definite answer about place and time of domestication.

Keywords: *Canis familiaris*, *canis 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 aim 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 Chinese Researchers Indicates Yangtze River Basin (2006-2010)

In a study Japanese and Asian dog breeds were searched by using phylogenetic analysis. The results claimed that the first domesticated dogs entered to Japan from southern or northern Asia and those dogs spread throughout Japan. Later than some other dogs were brought to Japan from Korean Peninsula and crossbred with the original dog breeds [12]. Ryabinina

published two articles about Asian dog breeds in 2006. He suggested that the genetic diversity was high in the Central Asian Shepherd and the Northern Caucasian Volkodav and but low in the Caucasian Shepherd Dogs. Haplotypes of groups A, B, C, and E/W had been found in Central Asian Shepherd, haplotypes of groups A and B, in Caucasian Shepherd Dogs. The data proved a gene flow from Scandinavian dog populations to the Northern Caucasus. As a result of the analysis it was clear that breeds of the Caucasian Shepherd, Northern Caucasian Volkodav, Central Asian Shepherd, Turkish Akbash Shepherd and Turkish Kangal (Karabash) Shepherd were combined into a single group with an extremely low degree of differentiation [13]. Ryabinina examined another study and compared to Asian dogs with European dogs. Additionally, it was determined in this study that there were extremely close phylogenetic relationships in group of Asian guardian dog breeds and close relation to this group breed German Shepherd dog

and group “Laika”. One of Portuguese breeds of Serra da Estrela Mountain Dog revealed more relation to Asian guardian dogs than to other Portuguese breeds. Breed groups of Central Asian Sheepdog, Northern Caucasian Volkodav and Laika characterized by relatively high level of genetic diversity in contrast with Caucasian Ovtcharka [14].

Natanaelsson *et al.* [15] conducted a survey to detect Y chromosomal DNA in dogs. The search team claimed that the 24159 bp of dog Y-chromosome sequence could be used for population genetic studies. They also sequenced 14437 bp in a worldwide collection of dogs, identifying 14 SNPs for future SNP analyses, and giving a first description of the dog Y-chromosome phylogeny [15]. A study came through to analyze the origin of contemporaneous breeds. In the study the analysis of paternally inherited Y chromosome markers combined with maternally inherited mitochondrial DNA and biparentally inherited autosomal microsatellite markers in both domestic dogs and their wild ancestor, the gray wolf. The results indicated that there was a sex bias in the origin of breeds, with fewer males than females contributing genetically, which clearly differed from the breeding patterns in wild gray wolf populations where both sexes had similar contributions. Moreover, a comparison of mitochondrial DNA and Y chromosome diversity in dog groups showed that paternal lineages were more differentiated among groups than maternal lineages. This result demonstrated a lower exchange of males than of females between breeds belonging to different groups, which illustrated how breed founders may have been chosen [16]. Björnerfeldt *et al.* realized an experiment to sequence the complete mitochondrial DNA genome in 14 dogs, six wolves, and three coyotes. They claimed that dogs had accumulated nonsynonymous changes in mitochondrial genes at a faster rate than wolves, leading to elevated levels of variation in their proteins. This result suggested that a major consequence of domestication in dogs was a general relaxation of selective constraint on their mitochondrial genome [17].

Wayne and Ostrander revealed that newly developed genomic resources had expanded the understanding of canine evolutionary history and dog origins. They also suggested that the domestication involved genetic contributions from multiple populations of gray wolves probably through backcrossing. The advent of controlled breeding practices had segregated genetic variability into distinct dog breeds that possessed specific phenotypic traits. As a result genome-wide association and selective sweep scans allowed the discovery of genes underlying breed-specific characteristics. The dog was finally emerging as a novel resource for studying the genetic basis of complex traits, including behaviour [18]. An experimental study was carried out to analyze the mitochondrial DNA (mtDNA) control region variation

within and among breeds. In the study 125 domestic dogs containing 43 breeds, as well as one coyote and two wolves were sequenced. As a result 40 informative variable sites were identified that described 45 haplotypes, 29 of which were observed only once [19].

Geyer *et al.* [20] carried out an analyze to investigate the nt230(del4) MDR1 mutation in White Swiss Shepherd dogs. The results showed that MDR1 locus was located at 16.6 Mb, so two microsatellites were flanking each the MDR1 locus. This marker order was different from the genetic map applied by Neff *et al.* [21]. The results also revealed that among the analyzed White Swiss Shepherd dogs, one was homozygous for the MDR1(-) mutant allele, three were heterozygous, and three dogs exhibited the wild type MDR1(+) allele [20]. A study was materialized for Hardy-Weinberg Expectations in some canine breeds. In the study 109 single-nucleotide polymorphisms (SNPs) were genotyped from 13 genes in a cohort of 894 dogs encompassing 33 breeds. Analysis of the entire cohort of dogs revealed a significant deviation away from HWE for all SNPs tested ($P, 0.00001$). In additional analysis of the cohort stratified by breed and subbreed indicated that the majority of the markers complied with HWE expectation. This suggested that canine case-control association studies could be valid if performed within defined breeds [22].

An analysis exerted to research phylogenomics of the domestic dog, dhole, fennec fox, gray fox, corsac fox, and red fox by using chromosome painting methods. The integrated map demonstrated an extensive conservation of whole chromosome arms across different canid species [23]. Parra *et al.* reported that compared histories with genetic relationships among five modern breeds of pointing dogs (English Setter, English Pointer, Epagneul Breton, Deutsch Drahthaar and German Shorthaired Pointer) were collected in Spain by using mitochondrial, autosomal and Y-chromosome information. In the study 236 alleles in autosomal microsatellites, four Y-chromosome haplotypes and 18 mitochondrial haplotypes were identified. The modern English Setter, thought to have arisen from the Old Spanish Pointer, was the first breed to cluster independently when using autosomal markers and seemed to share a common maternal origin with the English Pointer and German Shorthaired Pointer. The result of analysis of mitochondrial DNA sequence showed the isolation of the Epagneul Breton, which had been formally documented, and showed Deutsch Drahthaar as the result of crossing the German Shorthaired Pointer with other breeds [24]. A Chinese research team succeeded a study to determine origin and phylogenetic analysis of Tibetan Mastiff additionally using 12 breeds of other dog breeds, grey wolves and coyotes as outgroups based on the mtDNA sequence. Tibetan Mastiff, domestic dog breeds, and grey wolves were clustered into a group and coyotes were clustered in a group separately. The research team

claimed that the approximate divergence time between Tibetan Mastiff and grey wolf was 58,000 years before the present, and the approximate divergence time between other domestic dogs and grey wolf was 42,000 YBP. This indicated that the time of origin of the Tibetan Mastiff was earlier than that of the other domestic dogs [25].

A genomic architecture of segmental duplications and associated copy number variants study was carried out in domesticated dogs. In the study the first systematic and genome-wide analysis of segmental duplications and associated copy number variants were calculated in the modern domesticated dogs which exhibits considerable morphological, physiological, and behavioural variation. They also designed high-density tiling arrays spanning all predicted segmental duplications and performed aCGH in a panel of 17 breeds and a gray wolf. As a result copy number variants covered 429 genes that were involved in a wide variety of biological processes such as olfaction, immunity, and gene regulation [26]. A study was realized for mutation in melanocortin gene in gray wolves. The observed result indicated that the melanistic K locus mutation in North American wolves derived from past hybridization with domestic dogs. Moreover it had risen to high frequency in forested habitats, and exhibits a molecular signature of positive selection. The same mutation also caused melanism in the coyote and Italian gray wolves. Hence this results proved that how traits selected in domesticated species could influence the morphologic diversity of their wild relatives [27].

Coat colour variation was investigated in a study because of being essential characteristics of domestic dog breeds. In the study genome-wide association studies executed more than 1000 dogs from 80 domestic breeds to identify genes associated with canine fur phenotypes and distinct mutations in three genes, RSPO2, FGF5, and KRT71 (encoding R-spondin-2, fibroblast growth factor-5, and keratin-71, respectively) were detected [28]. Pang et al. fished for 582 bp of the control region by using 1.576 dogs and 40 wolves and for 16.195 bp of mtDNA by using 169 dogs and 8 wolves from all over the World. After observed results the suggested that the dog had a single origin in southern China less than 16.300 years ago [29]. An experimental study was carried out in African village dogs by comparing some other dog breeds of the World. In the study 318 village dogs from 7 regions in Egypt, Uganda, and Namibia were researched by measuring genetic diversity >680 bp of the mitochondrial D-loop, 300 SNPs, and 89 microsatellite markers. The team also analyzed breed dogs, including putatively African breeds (Afghan hounds, Basenjis, Pharaoh hounds, Rhodesian ridgebacks, and Salukis), Puerto Rican street dogs, and mixed breed dogs from the United States. Village dogs from most African regions appeared genetically distinct from non-native breed and mixed-

breed dogs, although some individuals clustered genetically with Puerto Rican dogs or United States breed mixes instead of with neighboring village dogs. The researchers emphasized that there was a similar mtDNA haplotype diversity in African and East Asian village dogs, therefore the hypothesis of an East Asian origin for dog domestication was suspicious [30].

In 2010 there were several researches about dog domestication and origin. The Insulin-like growth factor 1 (IGF1) small dog haplotype was studied derived from Middle Eastern grey wolves. The results suggested that grey wolf haplotypes from the Middle East had higher nucleotide diversity suggesting an origin there. Moreover PCA and phylogenetic analyses suggested a closer kinship of the small domestic dog IGF1 haplotype with those from Middle Eastern grey wolves. In accordance with past archeological studies, this molecular analysis was consistent with the early evolution of small size in dogs from the Middle East [31]. A study was conducted to research the IGF1 small dog haplotype in Middle Eastern grey wolves like study of Gray *et al.* [31]. The results suggested that comparisons between European dog breeds and village dogs or wolves would only capture variation and similarities relative to the European dog gene pool [32]. Again Klütsch and her team realized another experiment about dog-wolf hybridization in Scandinavia. The team analysed 582 bp of the mtDNA control region for 514 dogs of breeds earlier shown to harbour d1 and possibly related northern spitz breeds. The data demonstrated that subclade d1 originated in northern Scandinavia, at most 480–3000 years ago and through dog-wolf crossbreeding rather than a separate domestication event [33]. Domestic dog populations USA were investigated regarding geographic differences in mtDNA distribution in USA. According to observed results 91% of the variation was present within the regional dog populations. Based on those analyses, the significance of regional canine HV1 haplotype distributions and frequencies revealed further the value of regional and mixed breed canine mtDNA in forensic investigations in the US [34].

Akey *et al.* [35] realized an experiment for tracking footprints of artificial selection in the dog genome in 275 dogs from 10 breeds. The results proved a first-generation map of selection in the dog, illustrated how such maps could rapidly inform the genetic basis of canine phenotypic variation, and provided a framework for delineating the mechanistic basis of how artificial selection promotes rapid and pronounced phenotypic evolution. Boyko *et al.* implemented an analysis for a simple genetic architecture underlined morphological variation using 915 dogs from 80 domestic breeds, 83 wild canids and 10 outbred African shelter dogs. The results indicated that there was the efficacy of mapping multiple traits in the domestic dog using a database of genotyped individuals

and additionally highlight the important role human-directed selection had played in altering the genetic architecture of key traits in this important species [36]. vonHoldt et al looked through genome-wide SNP and haplotype analyses related with a rich history underlying dog domestication. The research team revealed that Middle Eastern wolves were a critical source of genome diversity, although interbreeding with local wolf populations clearly occurred elsewhere in the early history of specific lineages. The evolution of modern dog breeds also seemed to have been an iterative process that drew on a limited genetic toolkit to create remarkable phenotypic diversity [37].

Recent Studies (2011-2014)

Although dog and wolf lineages are difficult to separate in terms of nuclear genes, mitochondrial lineages are clearly distinguishable for the two species. A study revealed 12 dog and 4 wolf mtDNA control region haplotypes. The results demonstrated that none of the haplotypes were shared, confirming that mtDNA control region haplotypes could be used to discriminate between Croatian wolves and dogs, and to confirm the maternal ancestry of putative hybrids. The sequences of the two wolf-like animals clearly grouped into a dog cluster [38]. A PhD thesis was completed for the molecular ecology of Australian wild dogs named as. The thesis results found reinforce the variability in Australian wild dogs previously demonstrated by studies of diet and movements, and provided a novel and comprehensive overview of gene flow both among wild dogs and between dingoes and domestic dogs [39]. Also Oskarsson et al investigated Australian dogs regarding mtDNA by comparing Southeast Asian and Polynesian dogs. In the study haplotypes of A29, Arc1 and Arc2 were searched and all three haplotypes were found in South China, Mainland Southeast Asia and Indonesia but absent in Taiwan and the Philippines. The results also indicated that the mtDNA diversity among dingoes was an introduction to Australia 4600–18 300 years ago. These results asserted that Australian dingoes and Polynesian dogs originated from dogs introduced to Indonesia via Mainland Southeast Asia before the Neolithic, and not from Taiwan together with the Austronesian expansion [40].

An experiment was carried out to fish the origin of the Tibetan Mastiff and species identification of *Canis* regarding on mitochondrial cytochrome c oxidase subunit I (COI) gene and COI barcoding. According to phylogenetic trees and networks studies domestic dogs had four maternal origins (A to D) and that the Tibetan Mastiff originated from Clade A. This result supported the theory of an East Asian origin of domestic dogs. In additionally clustering analysis and networking revealed the presence of a closer relative between the Tibetan Mastiff and the Old English sheepdog, Newfoundland, Rottweiler and Saint Bernard. This result demonstrated that many well-known large breed dogs in the world, such as the Old

English sheepdog, might have the same blood lineage as that of the Tibetan Mastiff [41]. Another Chinese research team conducted an analysis to investigate origins of domestic dog in southern east Asia supported by analysis of Y-chromosome DNA. They used 151 dogs from various breeds, 12 wolves and 2 coyotes. The team found 28 haplotypes distributed in five haplogroups in which two other haplogroups were primarily restricted to East Asia. They claimed that Asia South of Yangtze was the principal, and possibly sole region of wolf domestication, that a large number of wolves were domesticated, and that subsequent dog–wolf hybridisation contributed modestly to the dog gene pool [42].

Brown *et al.* [43] searched the phylogenetic distinctiveness of Middle Eastern and Southeast Asian village dogs regarding Y Chromosomes Illuminates Dog Origins. In the study 495 village dogs/dingoes from the Middle East and Southeast Asia, and 138 dogs from more than 35 modern breeds were used. According to observed results the importance of village dogs could be used to further elucidate origins and spread of the domestic dog. Ardalan et al. [44] examined the mtDNA among Southwest Asian dogs which contradicted independent domestication of wolf, but implied dog–wolf hybridization by using 582 dogs from southwest Asia. They compared to the results of 582 dogs with 1.556 Old World and they suggested that 97.4% of Southwest Asian dogs carried haplotypes belonging to a universal mtDNA gene pool, but that only a subset of this pool, five of the 10 principal haplogroups, was represented in Southwest Asia.

In 2012 Ardalan et al. [45] realized another experiment for narrow genetic basis for the Australian dingo confirmed through analysis of paternal ancestry. The genetic evidence results demonstrated that a very restricted introduction of the first dingoes into Australia, possibly from New Guinea and moreover they were isolated feral dogs. Caprola and Savolainen [46] enforced an analysis for extensive phenotypic diversity among South Chinese dogs. The observed results submitted that the diverse morphologies of European dogs might have been formed from genetic “building blocks” still present in the dog population of rural southern China.

Recently Pedersen *et al.* published a study as the effects of dog breed development on genetic diversity and the relative influences of performance and conformation breeding. They selected 8 dog breeds including Standard Poodle, Italian Greyhound, show and field English Setter, Red Setter, German Shorthaired and Wirehaired Pointers. According to results compared with their village dog relatives, all modern breed dogs exhibit reduced genetic diversity. Genetic diversity was even more reduced among breeds under selection for show/conformation [47]. Pertoldi et al. investigated Danish dog breeds including Danish

Spitz, Danish-Swedish Farm Dog, Broholmer, Old Danish Pointing Dog, and Greenland Dog. The results interestingly demonstrated that the breed of Greenland Dog with a tenfold higher census population size compared to the other breeds had the lowest within-breed genetic variation, emphasizing that census size was a poor predictor of genetic variation [48]. Sacks et al examined an analysis by using Y chromosome of Dingoes and Southeast Asian Village dogs and created a theory for expansion of dogs from this region to the west and north. Sacks obviously accepted that the earliest archeological evidence of ancient dogs was discovered in Europe and the Middle East, some 5–7 millennia before that from Southeast Asia. However mitochondrial DNA analyses suggested that most modern dogs originated from Southeast Asia. This case had fueled the controversial hypothesis that dog domestication originated in this region despite the lack of supporting archeological evidence. The research team proposed and investigated with Y chromosomes an alternative hypothesis for the proximate origins of dogs from Southeast Asia. The hypothesis was that a massive Neolithic expansion of dogs from this region happened and they largely replaced more primitive dogs to the west and north. The observed data suggested that the Dingoes exhibited a unique haplogroup characterized by a single distinguishing SNP mutation and 14 STR haplotypes. In addition the age of the European haplogroup was estimated to be only 1.7 times older than that of the dingo population, suggesting an origin during the Neolithic rather than the Paleolithic as predicted by the Southeast Asian origins hypothesis. As a consequence they hypothesized that isolation of Neolithic dogs from wolves in Southeast Asia was a key step accelerating their phenotypic transformation, enhancing their value in trade and as cargo, and enabling them to rapidly expand and replace more primitive dogs to the West. They also claimed that dingoes could have arrived in Australia directly from Taiwan, independently of later dispersals of dogs through Thailand to Island Southeast Asia [49].

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.

REFERENCES

1. Dinets V. The History of Dog Domestication. 2007.

2. Vila C, Maldonado JE, Wayne RK. Phylogenetic Relationships, Evolution, and Genetic Diversity of the Domestic Dog. *J Hered.* 1999; 90 (1): 71-7.
3. Wayne RK, Leonard JA, Vila C. Genetic Analysis of Dog Domestication, in M. Mashkour (ed.) *Equids in Time and Space: 279-293.* Oxbow Books, University of California Press, London. 2006.
4. Yilmaz O. Turkish Native Horse Breeds and a Conservation Policy. *Yuzuncu Yil Universitesi Ziraat Fakultesi Dergisi.* 2012; 22 (2): 117-133.
5. Yilmaz O, Savas T, Ertugrul M, Wilson RT. The Domestic Livestock Resources Of Turkey: Inventory Of Pigeon Groups And Breeds With Notes On Breeder Organizations. *World's Poultry Science Journal.* 2013; 69 (2): 265-278.
6. Driscoll CA, Macdonald DW. Top Dogs: Wolf Domestication and Wealth. *J Biol.* 2010; 9 (2): 10.
7. Honeycutt RL. Unraveling the Mysteries of Dog Evolution. *BMC Biology.* 2010; 8(1), 20.
8. Shearman JR, Wilton AN. Origins of the domestic dog and the rich potential for gene mapping. *Genetics research international.* 2011 Jan 17;2011.
9. Vaughan TA, Ryan JM, Czaplewski NJ. *Mammalian Domestication (In Mammalogy).* Jones & Bartlett Publishers, USA. 2013
10. Serpell JA. Canid evolution: From wolf to dog (in Grzimek's Animal Life Encyclopedia, ed. B. Grzimek). Cengage Learning, Cambridge University Press, Cambridge, UK. 2011.
11. Larson G, Burger J. A Population Genetics View of Animal Domestication. *Trends in Genetics.* 2013; 29 (4): 197-206.
12. Tanabe Y. Phylogenetic Studies of Dogs with Emphasis On Japanese And Asian Breeds. *Proceedings of the Japan Academy, Series B.* 2006; 82(10), 375-387.
13. Ryabinina OM. Mitochondrial DNA variation in Asian Shepherd Dogs. *Genetika.* 2006a; 42 (7): 917-920.
14. Ryabinina OM. Genetic Diversity and Phylogenetic Relationships in Groups of Asian Guardian, Siberian Hunting and European Shepherd Dog Breeds. *Comparative and Evolutionary Genomics and Proteomics, Proceedings of the Fifth International Conference on Bioinformatics of Genome Regulation and Structure.* 2006b; 3: 225-228.
15. Natanaelsson C, Oskarsson M, Angleby H, Lundeberg J, Kirkness E, Savolainen P. Dog Y chromosomal DNA Sequence: Identification, Sequencing And SNP Discovery. *BMC Genet.* 2006; 7:45.
16. Sundqvist AK, Björnerfeldt S, Leonard JA, Hailer F, Hedhammar Å, Ellegren H, Vilà C. Unequal Contribution Of Sexes In The Origin Of Dog Breeds. *Genetics.* 2006; 172(2): 1121-1128.
17. Björnerfeldt S, Webster MT, Vilà C. Relaxation of selective constraint on dog mitochondrial DNA

- following domestication. *Genome Research*, 2006; 16 (8): 990-994.
18. Wayne RK, Ostrander EA. Lessons Learned From the Dog Genome. *Trends Genetic*, 2007; 23 (11): 557-567.
 19. Gundry RL, Allard MW, Moretti TR. Mitochondrial DNA Analysis of the Domestic Dog: Control Region Variation Within and Among Breeds. *J Forensic Science*, 2007; 52 (3): 562-572.
 20. Geyer J, Klintzsch S, Meerkamp K, Wöhlke A, Distl O, Moritz A, Petzinger E. Detection of the nt230(del4) MDR1 Mutation In White Swiss Shepherd Dogs: Case Reports Of Doramectin Toxicosis, Breed Predisposition, And Microsatellite Analysis. *Journal of Veterinary Pharmacology and Therapeutics*, 2007; 30(5), 482-485.
 21. Neff MW, Broman KW, Mellersh CS. A Second-Generation Genetic Linkage Map of the Domestic Dog, *Canis familiaris*. *Genetics*, 1999; 151: 803-820.
 22. Short AD, Kennedy LJ, Barnes A, Fretwell N, Jones C, Thomson W, Ollier WER. Hardy-Weinberg Expectations in Canine. *Journal of heredity*, 2007; 98(5), 445-451.
 23. Graphodatsky AS, Perelman PL, Sokolovskaya NV. Phylogenomics of the Dog And Fox Family (Canidae, Carnivora) Revealed By Chromosome Painting. *Chromosome Research*, 2008; 16(1): 129-143.
 24. Parra D, Méndez, S, Cañón J, Dunner S. Genetic Differentiation in Pointing Dog Breeds Inferred from Microsatellites and Mitochondrial DNA Sequence. *Anim Genet*, 2008; 39 (1): 1-7.
 25. Li Q, Liu Z, Li Y. Origin and Phylogenetic Analysis Of Tibetan Mastiff Based On The Mitochondrial DNA Sequence. *J Genet Genomics*. 2008; 35 (6): 335-40.
 26. Nicholas J, Cheng Z, Ventura M. The Genomic Architecture of Segmental Duplications and Associated Copy Number Variants in Dogs. *Genome Research*. 2009; 19:491-499.
 27. Anderson TM, von Holdt BM, Candille SI. Molecular and Evolutionary History of Melanism in North American Gray Wolves. *Science*. 2009; 323 (5919): 1339-1343.
 28. Cadieu E, Neff MW, Quignon P. Coat Variation in the Domestic Dog is governed by Variants in Three Genes. *Science*, 2009; 326 (5949) : 150-153.
 29. Pang J-F, Kluetsch C, Zou X-J. MtDNA Data Indicate a Single Origin for Dogs South of Yangtze River, Less Than 16,300 Years Ago, from Numerous Wolves. *Molecular Biology Evolution*. 2009; 26(12): 2849-2864.
 30. Boyko AR, Boyko RH, Boyko CM. Complex Population Structure In African Village Dogs And Its Implications For Inferring Dog Domestication History. *Proc Natl Acad Sci U S A*. 2009; 106:13903-13908.
 31. Gray MM, Sutter NB, Ostrander EA, and Wayne RK. The IGF1 Small Dog Haplotype Is Derived From Middle Eastern Grey Wolves. *BMC Biol*. 2010; 24 (8): 16.
 32. Klütsch CFC, Caprona MDC. The IGF1 Small Dog Haplotype Is Derived From Middle Eastern Grey Wolves: A Closer Look At Statistics, Sampling, And The Alleged Middle Eastern Origin Of Small Dogs. *BMC Biol*. 2010; 8: 119.
 33. Klütsch CFC, Seppala EH, Fall T, Uhlén M, Hedhammar A, Lohi H, Savolainen P. Regional Occurrence High Frequency But Low Diversity Of Mitochondrial DNA Haplogroup D1 Suggests A Recent Dog-Wolf Hybridization In Scandinavia. *Animal Genetic*, 2011; 42(1):100-3.
 34. Smalling BB, Satkoski JA, Tom BK. Geographic Differences in Mitochondrial DNA Distribution Among United States Domestic Dog Populations. *The Open Forensic Science Journal*, 2010; 3: 22-32.
 35. Akey JM, Ruhe AL, Akey DT. Tracking footprints of artificial selection in the dog genome. *Proceedings of the National Academy of Sciences of the United States of America*, 2010; 107 (3): 1160-1165.
 36. Boyko AR, Quignon P, Li L, Schoenebeck JJ. A Simple Genetic Architecture Underlies Morphological Variation in Dogs. *PLoS biology*, 2010; 8(8): e1000451.
 37. Von Holdt BM, Pollinger JP, Lohmueller KE. Genome-Wide SNP And Haplotype Analyses Reveal A Rich History Underlying Dog Domestication. *Nature*, 2010; 464 (7290): 898-902.
 38. Sindicic M, Gomercic T, Galov A. Mitochondrial DNA Control Region as a Tool for Species Identification and Distinction between Wolves and Dogs from Croatia. *Veterinarski Archiv*, 2011; 81: 249-258.
 39. Stephens D. The Molecular Ecology of Australian Wild Dogs: Hybridization, Gene Flow and Genetic Structure At Multiple Geographic Scales (PhD Dissertation). The University of Western Australia, Perth. 2011.
 40. Oskarsson MCRO, Klütsch, CFC, Boonyaparakob U, Wilton A, Tanabe Y, Savolainen P. Mitochondrial DNA Data Indicate an Introduction Through Mainland Southeast Asia for Australian Dingoes and Polynesian Domestic Dogs. 2011.
 41. Li Y, Zhao X, Pan Z. The Origin of the Tibetan Mastiff and Species Identification of *Canis* Based On Mitochondrial Cytochrome C Oxidase Subunit I (COI) Gene and COI Barcoding. *animal*, 2011; 5: 1868-1873.
 42. Ding ZL, Oskarsson M, Ardalan A. Origins of Domestic Dog in Southern East Asia is Supported By Analysis of Y-chromosome DNA. *Heredity*. 2011; 108: 507-514.
 43. Brown SK, Pedersen NC, Jafarishorijeh S. Phylogenetic Distinctiveness of Middle Eastern and Southeast Asian Village Dog Y Chromosomes

- Illuminates Dog Origins. *PLoS One* 2011; 6:e28496.
44. Ardalan A, Kluetsch CFC, Zhang AB. Comprehensive Study of Mtdna among Southwest Asian Dogs Contradicts Independent Domestication of Wolf, But Implies Dog–Wolf Hybridization. *Ecology and Evolution*. 2011; 1:373–385.
 45. Ardalan A, Oskarsson M, Natanaelsson C, Wilton AN, Ahmadian A, Savolainen P. Narrow Genetic Basis For The Australian Dingo Confirmed Through Analysis Of Paternal Ancestry. *Genetica*. 2012; 140: 65–73.
 46. Crapone de Caprona MD, Savolainen P. Extensive Phenotypic Diversity among South Chinese Dogs. *Evolutionary Biology*. 2013.
 47. Pedersen NC, Liu H, Theilen GH, Sacks BN. The Effects of Dog Breed Development on Genetic Diversity and the Relative Influences of Performance and Conformation Breeding. *J Anim Breed Genet. Journal of Animal Breeding and Genetics*, 2013; 130(3), 236-248.
 48. Pertoldi C, Kristensen TN, Loeschcke V. Characterization of the Genetic Profile of Five Danish Dog Breeds. *Journal of animal science*, 2013; 91(11): 5122-5127.
 49. SacksBN, Brown SK, Stephens D, Pedersen NC, Wu JT, Berry O. Y chromosome Analysis of Dingoes and Southeast Asian Village Dogs Suggests a Neolithic Continental Expansion from Southeast Asia Followed by Multiple Austronesian Dispersals. *Mol. Biol. Evol.* 2013; 30 (5): 1103–1118.