

Review

Phylogenetic studies of dogs with emphasis on Japanese and Asian breeds

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Abstract: The first domestication of the dog occurred in East Asia, and major ancestor of the dog was a wolf subspecies, *Canis lupus chanco*. This finding derives from data on the nucleotide sequences of mtDNA and the frequency of genes controlling blood protein polymorphisms in various subspecies of wolves and dog breeds around the world. The results of the allele frequency distribution of genes controlling 16 blood protein polymorphisms, and the incidence of dogs possessing erythrocytes with high potassium (HK) in Japan, East Asia and Europe allowed us to postulate the following hypothesis about the origins of Japanese dogs and the history of their development. In the Jomon period the first dogs entered the Japanese archipelago from southern or northern continental Asia. These dogs eventually spread throughout Japan. Then, during the Yayoi and Kofun periods, other dogs were brought over via the Korean Peninsula, and crossbreeding occurred with the original dogs. The resulted offspring can be assumed to be the ancestors of most of the Japanese breeds that exist today. Ethological studies have revealed a significant breed difference in behavioral traits among canine breeds with Japanese dogs, showing more aggressive dispositions than most of European dogs.

Key words: Wolf ancestry of the dog; phylogeny of Japanese dogs; mtDNA; gene frequency; blood protein polymorphism; erythrocytes with high potassium (HK).

Relationship of humans and animals. All wild animals obtain their food by hunting other animals and/or gathering plants.

In the pre-agricultural era, humans fed themselves exclusively by hunting wild animals and gathering edible plants like the wild animals, and extracting foods. Around 20,000 years ago, humans developed a symbiotic relationship with wolves for their mutual benefits. Wolves watched and guarded their residence from wild nocturnal predators animals and cooperated in humans hunting wild animals. Wolves were tamed and evolved into dogs between 15,000 and 20,000 years of age.^{1), 2)}

Most relationships between man and the domesticated animals are modified commensalisms. Commensalism means a close association between two

species of organisms, one of which is benefited by the relationship and the other is neither benefited nor harmed, but it is not a partnership, meaning that in which both are mutually benefited. The relationship between humans and dogs is mutualism. The purpose of domestication of cats in Egypt about 4,000 years ago was to destroy parasitic mice and black rats devouring stored crops.¹⁾ The relationship of humans and cats becomes mutualism.

Domesticated animals were divided into three categories; Working or serving animals such as dogs, cats, horses; animals as raised for food such as sheep, goats, cattle, pigs, chickens and ducks; fiber product animals such as sheep and silkworm moths. Humans and ants are unique species, having developed such modified commensalisms with other species. Interestingly, humans are the most prosperous vertebrate species, implying that their prosperity greatly de-

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depends on other animals and plants, while ants are the most prosperous species among invertebrates.¹⁾

Wolf ancestry and domestication of dogs.

Wolves (*Canis lupus*) inhabit Eurasia and North America. There are five subspecies: *Canis lupus lupus*, *Canis lupus chanco*, *Canis lupus pallipes*, *Canis lupus arabs* and *Canis lupus panbasilens*. The first four inhabit Eurasia and the last one lives in northern part of North America.

Wolves have been considered to be the sole ancestor of domesticated dogs both morphologically^{3), 4)} and ecologically.⁴⁾ *Canis lupus lupus*, the largest inhabits Europe. *Canis lupus chanco*, the second largest lives in East Asia, and is currently limited to northern Asia. *Canis lupus pallipes*, the third largest makes its home in India and living in India and Southwest Asia. *Canis lupus arabs*, the smallest of the five, is native to Arabia, Israel and Syria. The last two subspecies, *Canis lupus arabs* and *Canis lupus pallipes*, especially the former were candidates for the precursors of dogs, mainly due to their smaller body size.¹⁾

Tsuda *et al.*⁵⁾ showed that extensive interbreeding occurred among multiple matriarchal ancestors during the domestication of dogs and a close relationship between dogs and wolves from inter- and intraspecies polymorphism in D-loop region (672-1bp) of mitochondrial DNA between dogs and wolves. Furthermore, one clade (A) containing the Chinese wolf (*Canis lupus chanco*) showed extensive variations while the other clade (B) showed only a slight variation (Fig. 1).

These results indicated that the ancestor of the domestic dog is the wolf, and that *Canis lupus chanco* was deeply involved in the domestication process of wolves. Vilá *et al.*^{6), 7)} showed that the wolf was the sole ancestor of the dog from mitochondrial DNA control region sequences (261 base pair length).

Mitochondrial DNA is always inherited strictly maternally.⁸⁾ Analyses of mitochondrial DNA polymorphisms and nucleotide substitutions are very useful for identifying matriarchal but not patriarchal lineages. Genetic analyses of protein polymorphisms are useful for detecting both lineages.

Tanabe *et al.*⁹⁾ electrophoretically and chromatographically examined the allele frequencies of 16 polymorphic blood protein loci in three subspecies of wolves; *Canis lupus chanco* (Mongolia), *Canis lupus pallipes* (Afghanistan) and *Canis lupus lupus* (Yugoslavia), and two populations of primitive dogs, *Ca-*

nis familiaris hallstromi (New Guinea singing dog) and *Canis familiaris dingo* (Australian dingo). The mode of inheritance of the alleles on 16 polymorphic and 11 monomorphic blood protein loci is given in Table I.

From the data given in Table II, significantly higher frequencies of esterase-2^F (*Es-2^F*), ganglioside monooxygenase^G (*Gmo^G*) and hemoglobin^A (*Hb^A*) were observed in *Canis lupus chanco* than in the other wolf subspecies.⁹⁾

Close relationships were observed among the allele frequencies at the locus of the three loci between *Canis lupus chanco* and Asian dog breeds (Table II), indicating *Canis lupus chanco* is an ancestor of Asian dogs.

Savolainen *et al.*¹⁰⁾ examined the mitochondrial DNA subsequence variation among wolves and dog populations worldwide. They established East Asian origin of the domestic dog based on a larger genetic variation in East Asia than in other regions and on the pattern of polymorphic variation.

All the data support that the first domestication of the dog occurred in East Asia, and that a major ancestor of the dog was a subspecies of wolf, *Canis lupus chanco*.

Migration and diversity of dogs. Dogs were domesticated in East Asia from East Asian wolves (*Canis lupus chanco*) more than 15,000 years ago. That date is estimated from the rate of molecular substitution of mitochondrial DNA,^{6), 7)} and the age of ancient dog remains.²⁾ Domesticated dogs accompanying people migrated and dispersed throughout the entire world.

It was that native American people (Amerinds) especially in North American Amerinds kept only dogs as the domesticated animal species, while the native people in South America kept dogs, and a few newly domesticated animals such as llamas, alpacas and guinea pigs. No Amerindians kept cattle, buffaloes, horses, sheep, goats, pigs or cats at the time of the Spanish and Portuguese conquest, confirming that dogs were domesticated in the pre-agricultural era.¹¹⁾

Recently, mitochondrial DNA sequences isolated from ancient dog remains from Latin America and Alaska showed that American native dogs originated from old world (East Asia) lineages of dogs that were accompanied by humans in their migration across the Bering Strait in the late Pleistocene age.¹²⁾

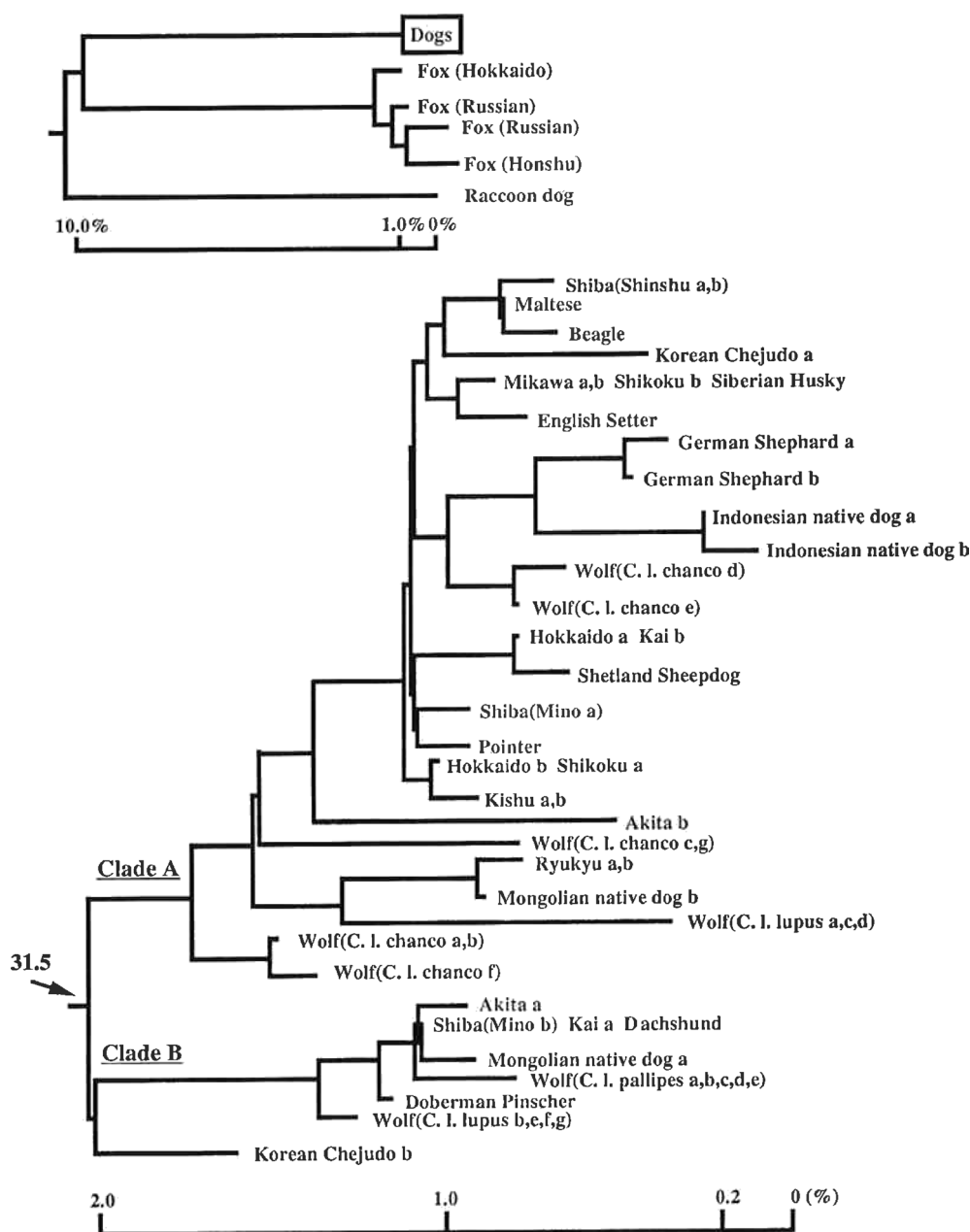


Fig. 1. Phylogenetic trees constructed by the neighbor-joining (NJ) methods for dogs, foxes, and a raccoon dog in the upper graph, and dogs and wolves in the lower graph. These trees are based on the sequence divergence with regard to the first 674 bp of the mtDNA. The arrow marks the rate of branch between two clades in the phylogenetic tree with 100 bootstrap replicates. The scale bar represents sequences divergences between animal species or breeds examined. From Fig. 2 in ref. 5).

Ancient breeds such as *Canis familiaris dingo* (dingoes) and *Canis familiaris hallstromi* (New Guinea singing dogs) were developed when human migrants and their domestic dogs reached Australia and New Guinea as early as 5,000 years ago.¹³⁾

Only one native dog breed, the Basenji, was preserved in Central Africa, and was brought to England

1895. Canine kept as hunting dogs and their ancestors were found in ancient Egypt.¹⁴⁾

The proposed migration routes of dogs are shown in Fig. 2.

Dogs were kept to watch for invaders and to cooperate humans in hunting in the pre-agricultural era. About 11,000–12,000 years ago, humans started

Table I. Modes of inheritance in the 27 blood protein loci (Modified from Table I in refs. 9), 16))

Protein	Abbreviation	Mode of inheritance ^{*)}
Enzymatic		
Plasma alkaline phosphatase	Akp	$Akp^A = Akp^B = Akp^C$
Plasma eserine resistant esterase	Es	$Es^A = Es^B = Es^C$
Plasma leucine aminopeptidase	Lap	$Lap^A = Lap^B$
Erythrocyte acid phosphate isomerase	Pac	$Pac^F = Pac^S$
Erythrocyte esterase-2	Es-2	$Es-2^S > Es-2^F$
Erythrocyte esterase-3	Es-3	$Es-3^A = Es-3^B$
Erythrocyte acid phosphate isomerase	GPI	$GPI^A = GPI^B = GPI^C = GPI^D$
Erythrocyte tetrazorium oxidase	To	$To^A = To^B$
Erythrocyte ganglioside monooxygenase	Gmo	$Gmo^g > Gmo^a$
Plasma amylase	Amy	not variable
Plasma esterase-fast	Es-f	not variable
Erythrocyte adenylate kinase	AK	not variable
Erythrocyte esterase-fast	Cell Es-f	not variable
Erythrocyte glucose- β -phosphate dehydrogenase	G-6-PD	not variable
Erythrocyte lactose dehydrogenase-A	LDH-A	not variable
Erythrocyte lactose dehydrogenase-B	LDH-B	not variable
Erythrocyte leucine aminopeptidase	Cell-Lap	not variable
Non-enzymatic		
Plasma albumin	Alb	$Alb^F = Alb^S$
Plasma postalbumin	Poa	$Poa^A = Poa^B = Poa^C$
Plasma proalbumin-3	Poa-3	$Poa-3^A = Poa-3^B$
Plasma prealbumin-1	Pa-1	$Pa-1^A = Pa-1^B = Pa-1^C$
Plasma pretransferrin	Ptf	$Ptf^A > Ptf^O$
Plasma transferrin	Tf	$Tf^A = Tf^B = Tf^C = Tf^D = Tf^E$
Erythrocyte Hemoglobin	Hb	$Hb^A = Hb^B$
Plasma prealbumin-2	Pa-2	not variable
Plasma postalbumin-2	Poa-2	not variable
Plasma slow α^2 macroglobulin	$\alpha 2$	not variable

^{*)} A=B indicates that A and B are codominant alleles.

A>B indicates that A is a dominant allele and B is a recessive one.

to keep sheep, goats and cattle for meat production. Dogs served as herders for such domesticated animals. Dogs were bred for the various other purposes such as hunting, guarding and working. Currently there are more than 400 dog breeds in the world.

Microsatellite DNA polymorphisms and nucleotide substitutions are useful for detecting matri-

archal and patriarchal lineages.

Parker *et al.*¹⁵⁾ surveyed microsatellite DNA nucleotide sequences of wolves and 85 domestic dog breeds, showing that dogs could be divided into main two groups, primitive dog breeds such as Chinese (Chinese Shar-pei and Chow Chow), Japanese (Shiba and Akita), North American (Siberian, Husky

Table II. Allele frequencies of three loci, erythrocyte ganglioside monooxygenase (Gmo), esterase-2 (Es-2) and hemoglobin (Hb) in three subspecies of wolves, New Guinea singing dog, dingo, and dog breeds and populations in Eurasia (Reconstructed from Tables 4-6 in ref. 9))

Species	No.	Gmo		Es-2		Hb	
		<i>Gmo</i> ^a	<i>Gmo</i> ^g	<i>Es-2</i> ^F	<i>Es-2</i> ^S	<i>Hb</i> ^A	<i>Hb</i> ^B
European wolf (<i>Canis lupus lupus</i>)* ¹⁾	9	1.000	0.000	0.000	1.000	0.000	1.000
East Asia (Chinese) wolf (<i>Canis lupus chanco</i>)* ²⁾	16	0.707	0.293	0.707	0.293	0.875	0.125
Indian wolf (<i>Canis lupus pallipes</i>)* ³⁾	6	1.000	0.000	0.000	1.000	0.000	1.000
New Guinea singing dog (<i>Canis familiaris hallstromi</i>)* ⁴⁾	5	1.000	0.000	0.000	1.000	0.000	1.000
Dingo (<i>Canis familiaris dingo</i>)* ⁵⁾	1	1.000	0.000	0.000	1.000	0.000	1.000
European dog (19 breeds)	848	1.000	0.000	0.164	0.836	0.030	0.970
Mongolian dog (2 breeds and 1 population)	302	0.953	0.047	0.867	0.133	0.998	0.002
Korean dog (2 breeds and 1 population)	394	0.555	0.445	0.598	0.402	0.827	0.173
Japanese dog (8 breeds and 15 populations)	1,798	0.860	0.140	0.432	0.568	0.193	0.807
Taiwan native dog (4 populations)	144	0.948	0.052	0.187	0.813	0.000	1.000
Bangladesh native dog (1 population)	60	0.929	0.071	0.000	1.000	0.000	1.000

*1) from Yugoslavia, *2) from Mongolia, *3) from Afghanistan, *4) from New Guinea, *5) from Australia.

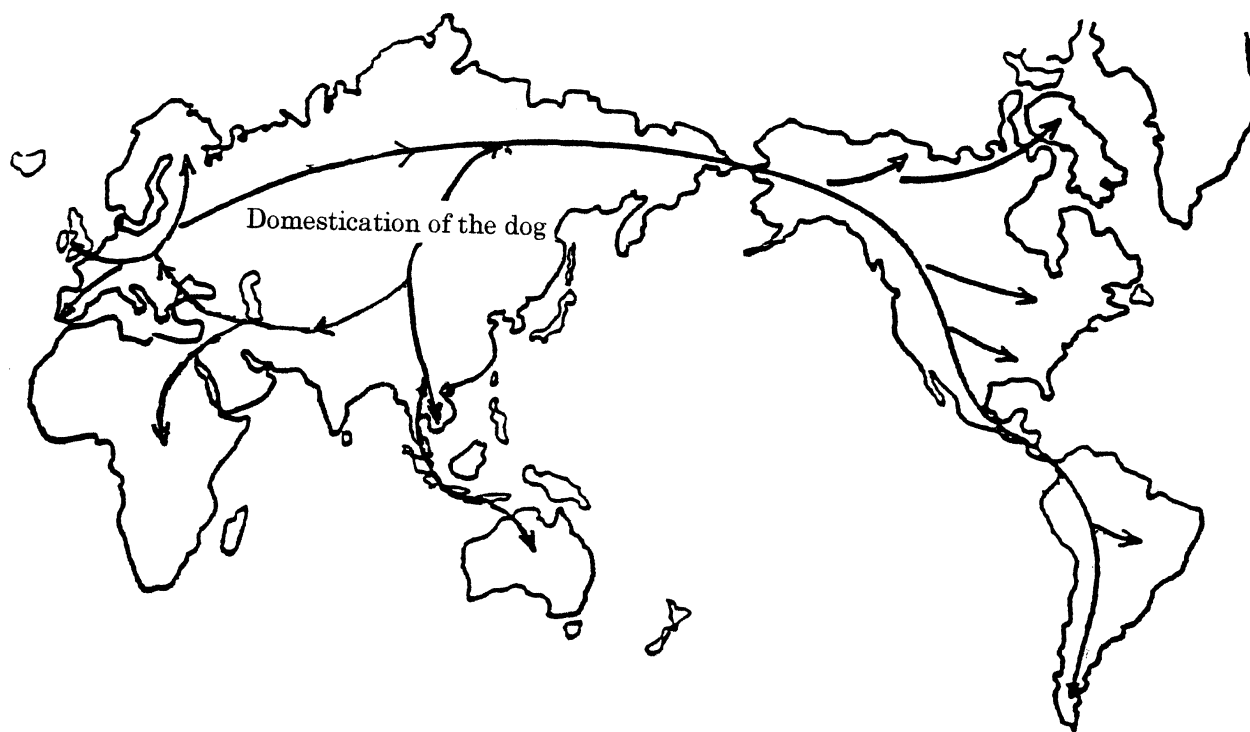


Fig. 2. Postulated migration routes and important locals in the domestication of the dog.

and Alaskan Malamute), a native African breed (Basenji), Southwest Asian breeds (Afghan Hound and Saluki) and modern dogs including most of European breeds, which in turn can be divided into three groups: herding dog breeds appeared first, fol-

lowed by hunting dogs and finally guarding dogs.

Origin of Japanese dogs and their association with Japanese people. Dogs have always migrated with people. The earliest-known migrants to Japan, the Jomon people, are thought to have

brought dogs to the Japanese archipelago some ten to twelve thousand years ago. The oldest dog skeletal remains discovered in Japan date from 9,500 before present (B.P.). The Jomon people, who lived by hunting and gathering, eventually settled in regions all over Japan, but mainly on Honshu, with dogs as their companions. The Jomon civilization lasted nearly ten thousand years, from 12,000 to 2,300 before present (B.P.) and through this period dogs seem to have been the sole domesticated animals. When their dogs died, their owners buried them.¹⁶⁾ This situation of the Jomon people was similar to that of North America Amerindians at the time of the Spanish and Portuguese conquest.

The early Japanese dog was small, roughly the same size as the present-day Shiba. Furthermore, the skulls are distinguished by a long muzzle and a shallow stop (the depression in area between the eyes that connects nose and forehead) or no stop at all. It is generally believed that these early dogs of the Jomon period are the ancestor of the six Japanese breeds found today, and that the prototype of the Japanese breeds was already established in the Jomon period, which was followed by the Yayoi period, marked by fresh wave migrants (now known as the Yayoi people) to Japan from the Korean Peninsula. The Yayoi period lasted for six hundred years. Skeletal remains of dogs from the Yayoi period, unearthed in the Kuwanae burial mounds in Oita Prefecture and the Yoshinogari burial mounds in Saga Prefecture, both of which are dated roughly to two thousand years ago, show distinct differences from the Jomon period dogs. Their skulls have a prominent stop, and their frames are slightly larger than the earlier type of dog. Such evidence suggests that in the Yayoi period a new type of dog came to Japan, along with the new wave of people from the continent. The care and devotion accorded to the burial of dogs in Jomon is no longer evident in sites dating from the Yayoi period (2300–1700 B.P.). Most dog skeletons are partial and the bone are scattered; the remains show cuts and seem to have had the flesh torn off. This suggests that in the Yayoi period dogs were eaten as food, and this habit would have been unthinkable among the Jomon.^{16), 17)}

In the years following Japan's opening to the West in 1868, ideas about animal welfare took hold, and any lingering practices of eating dog meat disappeared almost entirely. During the late nineteenth and early twentieth centuries, all sorts of dogs were

imported, particularly from Europe. In urban regions, crossbreeding between Japanese and foreign breeds proceeded rapidly, whereas in rural areas from Hokkaido to Kyushu, Japanese indigenous breeds, mainly used by hunters, were protected as local dogs and their genetic integrity preserved. In the latter half of the 1920s, amid growing national interest and pride in things Japanese, the movement to preserve Japanese dog breeds flourished. The Ministry of Education gave several Japanese dog breeds official recognition as "Natural monuments" (Protected Species): the Akita received this designation in 1931, the Kishu and Kai in 1934, the Shiba in 1936, and the Shikoku and Hokkaido in 1937. Preservation associations were established for each breed, and breed standardizations were formulated.¹⁷⁾

After the Second World War, thanks to the strenuous and unceasing efforts of conservation societies to restore, maintain, and preserve native breeds, Japanese dogs survived and began to flourish. One consolation in these difficult years was the fact that the indigenous breeds preserved as hunting dogs by hunters in the remote mountainous regions of Japan could be used to restore the breeds nation wide.

Apart from the six breeds above, several others should be mentioned here. One is the Chin, which was developed in Japan during the Edo period. The Chin was in fact brought to Japan from China many centuries before, and is altogether different in its morphology from other Japanese dogs, so its development does not seem to have involved any exchange of genes with indigenous Japanese dogs. There is also the Ryukyu dog, named for the subtropical island chain that arcs southwest from Kyushu. The Ryukyu dog is a breed of indigenous Japanese dog found in the Yanbaru region in the north of Okinawa Island and Ishigaki Island that followed its own separate course of development.¹⁷⁾

There are also the Mikawa dog of Tokushima Prefecture, and Satsuma dog of Kagoshima Prefecture, the latter of which has almost extinct. Both of these breeds have their own preservation movements, set up through the efforts of dog fanciers and enthusiasts.^{17), 18)}

Phylogenetic studies of Japanese dog breeds. Significant allele frequency differences among dog groups are shown in Table II.⁹⁾ Significantly higher allele frequencies of *Es-2^F* and *Hb^A* were observed in dogs from Korea, North Sakhalin, Mongolia and Indonesia than those from China, Tai-

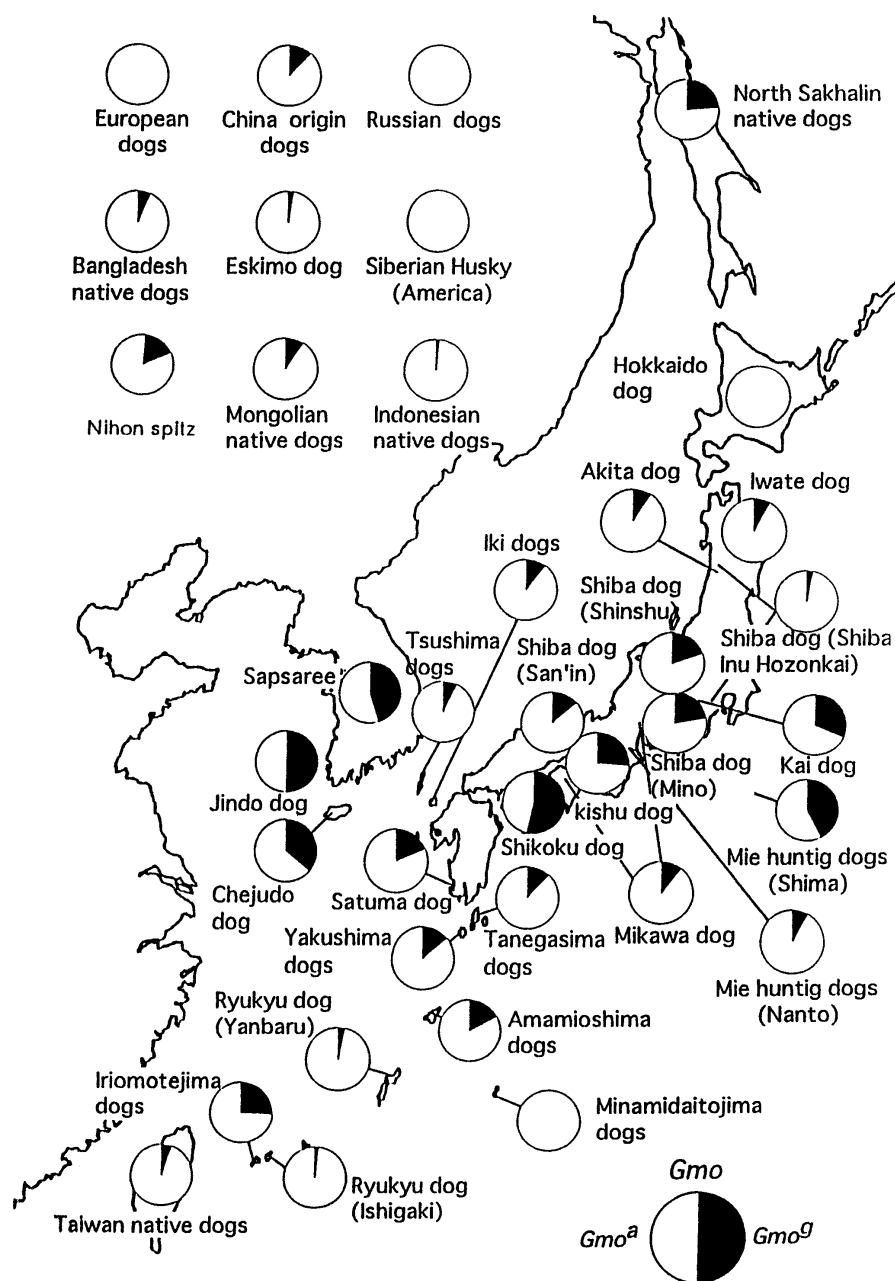


Fig. 3. Distribution of dog breeds in and around Japan by alleles on the *Gmo* (ganglioside monooxygenase). From Fig. 6 in ref. 9).

wan, Bangladesh, West Siberia (Russia) and Europe. The relatively higher allele frequency of Gmo^g was observed in the dogs of Northeast Asia than in those of Southeast Asia, West Siberia and Europe. The frequency of Gmo^g was very high (0.445) in Korean dogs, low (0.140) in Japanese dogs, and very low (0.013) in Indonesian dogs. Gmo^g was not found in West Siberian (Russia) nor European dogs. Distri-

bution of dog breeds and populations in and around Japan by alleles on the *Gmo* locus is illustrated in Fig. 3.⁹⁾

The presence of N-acetylneuramic acid (A-type) and glycolylneuramic acid (G-type) in dog erythrocyte membranes was discovered by Yamakawa's research group.^{19), 20)} The alleles of Gmo^a and Gmo^g on a locus (*Gmo*) control the phenotypes, with

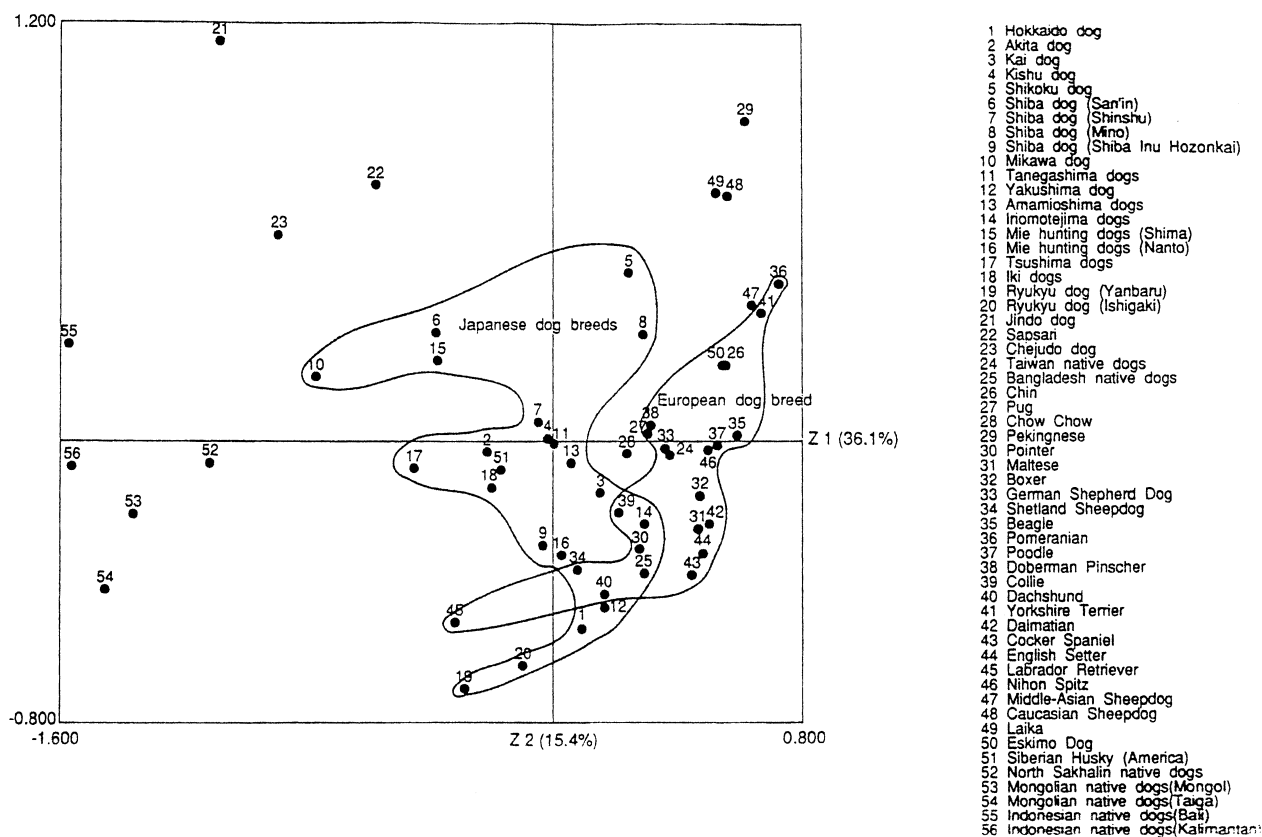


Fig. 4. Relative positions of 56 dog breeds and populations defined by the first (Z1) and the second (Z2) largest principal component of the distance matrix based on variance-covariance analysis of gene frequency at 16 polymorphic loci. The figure in parentheses shows the degree of contribution of the axis. From Fig. 10 in ref. 9).

the latter being found only in Japanese and East Asian dog breeds except the Hokkaido, a Japanese breed.^{9), 21), 22)}

To clarify genetic relationships among dogs, a scattered diagram of populations of the 56 dog breeds or populations plotted on the basis of the 1st and 2nd principal component scores are illustrated in Fig. 4⁹⁾ (methodology reference: Tanabe *et al.*²²⁾). The 1st and 2nd principal components account for 51.5%, of total variance. The figures clearly show close relationships among Mongolian, Indonesian, and North Sakhalin dogs, and among Korean and some Japanese dog breeds such as the Mikawa, the Shiba, Shikoku and the Shima lines of Mie hunting dogs. It is noteworthy that a close genetic relationship was observed between the Ryukyu living in the far south, and the Hokkaido living in the far north portion of Japan.

The cation composition in erythrocytes of Carnivores including dogs is high in Na and low in K

(LK), because of the lack of an Na, K-pump in its cell membrane. However, some Japanese dogs possessed red blood cells with high K and low Na (HK) due to the existence of an Na, K-pump. Fujise *et al.*²³⁾ examined the incidence of HK and LK phenotypes of erythrocytes in dog groups from 22 breeds or population in Japan and East Asian regions adjacent to Japan (Table III). The phenotype of high K (HK) erythrocytes, which is an autosomal recessive, was found in dog groups from 10 of 13 breeds or populations in Japan. The incidence of HK was 26 to 38% in the San'in-Shiba, Shinshu-Shiba and Akita breeds, and the gene frequencies of HK ranged from 0.513 to 0.612. The highest incidence (42%) was found in the Jindo breed from Korea, with a gene frequency of 0.652. Two other groups from Korea also possessed this HK variation. HK cells were not found in dogs from Taiwan, Indonesia, Mongolia or Sakhalin. And the HK phenotype is now clearly distributed throughout Japan and Korea. The gene mutation for HK

Table III. The incidence of HK (high potassium) and LK (low potassium) phenotypes of red cells and their frequency in dog groups from 22 breeds or populations in Japan and East Asia adjacent to Japan (From Table 1 in ref. 23)

Breed or population	Location	Number of dogs			Gene frequency	
		Total	Phenotype		LK	HK
Hokkaido ^{b)}	Hokkaido, Japan	40	38	2 (5.00) ^{a)}	0.776	0.224
Akita ^{b)}	Honshu, Japan	38	28	10 (26.3)	0.487	0.513
Shinshu-Shiba ^{b)}	Honshu, Japan	26	17	9 (34.6)	0.412	0.588
Mino-Shiba ^{b)}	Honshu, Japan	34	30	4 (11.8)	0.657	0.343
San'in-Shiba ^{b)}	Honshu, Japan	40	25	15 (37.5)	0.388	0.612
Kai ^{b)}	Honshu, Japan	35	32	3 (8.60)	0.707	0.293
Kishu ^{b)}	Honshu, Japan	40	37	3 (7.50)	0.726	0.274
Mikawa ^{b)}	Honshu, Japan	23	20	3 (13.0)	0.639	0.361
Shikoku ^{b)}	Shikoku, Japan	35	33	2 (5.70)	0.761	0.239
Iki ^{c)}	Kyushu, Japan	40	40	0 (0)	1.000	0.000
Tsushima ^{c)}	Kyushu, Japan	40	40	0 (0)	1.000	0.000
Satsuma ^{b)}	Kyushu, Japan	31	31	0 (0)	1.000	0.000
Ryukyu ^{b)}	Okinawa, Japan	40	39	1 (2.50)	0.842	0.158
Chejudo ^{c)}	Korea	40	34	6 (15.0)	0.613	0.387
Jindo ^{b)}	Korea	40	23	17 (42.1)	0.348	0.652
Sapsaree ^{b)}	Korea	31	29	2 (6.50)	0.746	0.254
Taiwan ^{c)}	Taiwan	40	40	0 (0)	1.000	0.000
Kalimantan ^{c)}	Indonesia	40	40	0 (0)	1.000	0.000
Bali ^{c)}	Indonesia	40	40	0 (0)	1.000	0.000
Sakhalin ^{c)}	Russia	40	40	0 (0)	1.000	0.000
Mongol ^{c)}	Mongolia	40	40	0 (0)	1.000	0.000
Taiga ^{c)}	Mongolia	28	28	0 (0)	1.000	0.000

^{a)} Incidence was shown in percent in parentheses.

^{b)} Pure breed.

^{c)} Dog population indigenous to locality.

might have first occurred in Korean dogs in ancient times, and might have been subsequently distributed in Japanese dogs that accompanied humans during migrations in Yayoi and Kofun periods to Japan.

Okumura²⁴⁾ determined sequences of mitochondrial DNA from 145 ancient dog remains (mainly bones) from the Jomon (3,000–2,400 B.P.), the Yayoi (2,400–1,700 B.P.), the Kofun (1,700–1,400 B.P.) and the Kamakura (1,300–800 B.P.) periods. The 198-bp ancient mtDNA was amplified from 74 dog samples, and the sequences were classified into 19 haplotypes comprising five modern haplotypes (M1, M2, M5, M10 and M11) identified in modern dogs together with ancient haplotypes showing unique sequences not observed in modern dogs. Haplotype M5 was

widely distributed in archaeological sites in northern Japan and Sakhalin, while haplotype M2 was detected from sites in southern Japan. Three major clusters (CL1 to CL3) were distinguished within the modern dog control region using phylogenetic analysis; all ancient dogs belonged to the CL1 cluster.

These results suggest that the CL1 cluster was probably distributed in the Japanese archipelago from the Jomon Period. Further haplotype M2 among the CL1 was likely distributed in Japan somewhat later (around the Yayoi period).

All the data on the gene flow of dogs in Japan and east Asian regions adjacent Japan support the following hypothesis: The first dogs entered the Japanese archipelago from southern or northern con-

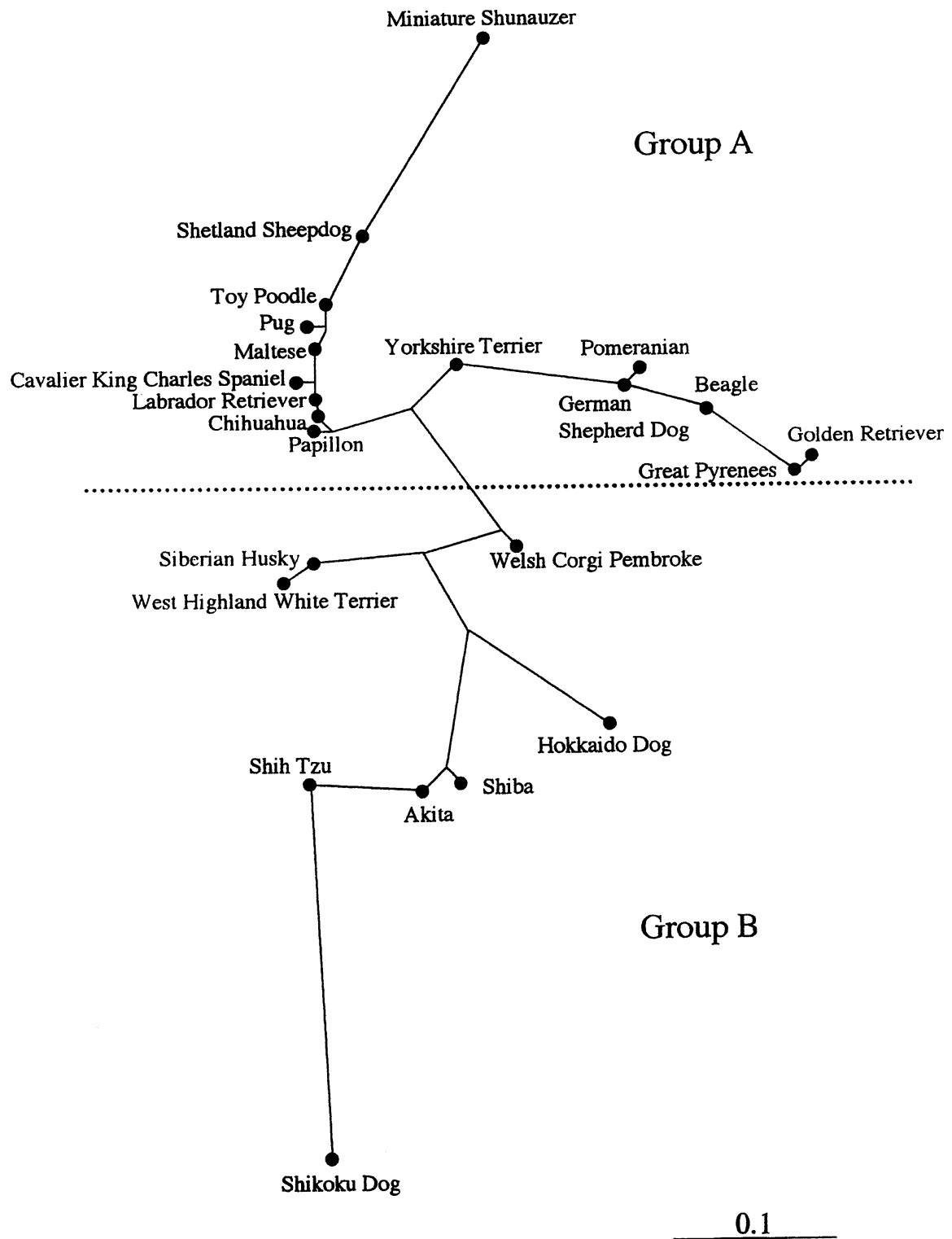


Fig. 5. A neighbor-joining (NJ) tree indicating the resemblance of allele composition of canine dopamine receptor D4 gene exon III made by the NJ method using genetic distance due to Reynolds *et al.*²⁹⁾ Breeds were divided into two main groups, A and B. From Fig. 2 in ref. 28).

tinental Asia. These dogs eventually spread throughout Japan. Then other dogs were brought over via the Korean Peninsula, and crossbreeding occurred with the original dog breeds. The resulting offspring can be assumed to be the ancestors of the Japanese breeds that exist today.

Ethological differentiation among dog breeds. Since the last parts of the 20th century in the developed countries, the practical functions of dogs are gradually diminishing in importance, while their behavioral attributes associated with the dog's companionship role in the human family are becoming increasingly relevant. In the modern society, dogs and cats are called companion animals. However, dogs are still used for herding, hunting and guarding livestock, as well as pulling sleds and contributing their unique skills to the police and armed forces.

Hart and Hart²⁵⁾ analyzed statistically the scores for behavioral traits, and found significant differences among dog breeds. Tanabe *et al.*²⁶⁾ and Tanabe and Yamazaki²⁷⁾ studied breed differences using the behavioral profiles of 19–31 dog breeds including six Japanese dog breeds. Profiles were obtained from the scores judged by small animal veterinarians, veterinary nurses and dog trainers. Highly significant breed differences were observed for all traits. High scores for aggressiveness, such as territorial defense, hostility toward other dogs and dominance over owners were clearly observed in six Japanese breeds, whereas those same breeds scored low estimates in friendly scores such as demand for affection, alacrity in obedience training, and playfulness, and adaptability to new owners, in contrast to friendly breeds such as of Labrador Retriever and Golden Retriever.

Ito *et al.*²⁸⁾ surveyed the allele frequency distribution of the canine dopamine receptor D4 gene (*DRD4*) exon III with nucleotide sequence polymorphisms in 23 breeds including a total of 1,535 individual unrelated dogs. A group of breeds in which the alleles 447b, 498 and 549 were frequent tended score higher aggression-related behavioral traits than those with frequent alleles 435 and 447a. Figure 5 shows a neighbor-joining tree indicating of composition of *DRD4* exon III made by the neighbor-joining method using genetic distance. Breeds were divided into two major groups, A and B. This figure shows a close relationship among four Japanese breeds, i.e. the Hokkaido, the Shiba, the Akita and the Shikoku and a Chinese breed the Shih Tzu, while breeds from the B group are more aggressive than A-group.

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Profile

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He received the Research Award of the Japanese Society of Animal Science in 1971, the Research Award of the Association of Agricultural Scientific Societies of Japan and the Yomiuri Agricultural Award in 1983, the Merit Award of Japan Poultry Science Association in 1992, the Purple Ribbon Medal in 1997, and the Order of the Sacred Treasure with Middle Lobe in 2004.

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