

Phylogenetic Studies on the Japanese Dogs,
with Emphasis on Migration Routes of the Dogs

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ABSTRACT

Phylogenetic relationships of Asian and European dog breeds or populations were studied by using the protein polymorphisms detected by electrophoretic and chemical analysis. Blood samples were taken from 3,445 dogs including ten Japanese, one Korean, three Chinese origin, Eskimo two Siberian and 43 European breeds and nine Japanese, one Taiwan, one Korean and one Bangladesh populations. Protein polymorphisms were observed in 14 loci: *Es*, *Lap*, *Akp*, *Hb*, *Es-2*, *Pac*, *GPI*, *To*, *Gmo*, *Pa-1*, *Alb*, *Poa*, *Poa-3* and *Tf*. A scattered diagram of the 43 dog breeds or populations on the basis of the 1st and 2nd principal component scores elucidates the existence of two close relationships among Taiwan native dogs, Chinese origin dog breeds, the Ryukyu dog and the Hokkaido (Ainu) dog, and those among Korean native breed (the Jindo) and population (Chejudo), and most of Japanese native breeds or populations in Honshu and Shikoku. There were two gene flows in dogs into Japan. The first was from southeast Asia through Taiwan and Ryukyu to all the Japanese Islands. And the second was from the Korean peninsula to the Japanese main Islands, except Hokkaido. It is assumed that the Hokkaido (Ainu) dog breed is a descendant of an old type of Japanese dog which was brought to Japan 10,000-12,000 years ago by Jomonese who came from southeast Asia. Most of the other Japanese native dog breeds or populations, except a breed (the Ryukyu) and some populations in Namsei (Ryukyu) islands are descendants of the hybrid between the old type of Japanese dogs and Korean origin dogs which were brought 1,700-2,300 years ago by the Yayoi migrants who came through the Korean peninsula.

Introduction

Findings of polymorphisms in blood proteins including enzymes (isozymes) in various domesticated animals have been enabled us to elucidate phylogenetic relationships of the breeds or populations of the animals. Dogs (*Canis familiaris*) are believed to have derived only from wolves, *Canis lupus* (Clutton-Brock, 1984), and are believed to be the oldest domesticated animal in preagricultural age (Turnbull and Reed, 1974; Payne, 1983). The relationship between man and dogs is partnership or companionship, and dogs always migrated with man since the ancient ages. The evidence suggests that it is possible to trace the route of migration of man by tracing the route of dog populations in the prehistoric ages. Phylogenetic relationships among the dog breeds with special reference to Asian dog breeds were studied by biochemical polymorphisms of the blood detected by electrophoretic and chemical analysis, and to intend to elucidate the origin of Japanese native dogs with emphasis on migration routes of the dogs.

Genes controlling blood protein polymorphisms in dogs

Blood samples were taken from the foreleg vein of 3,445 individual dogs including ten Japanese native breeds (pedigreed): the Hokkaido (which was called the Ainu dog because the Ainu tribe kept the breed), the Akita, the Kai, the Kishu, the Shikoku, the Shinshu Shiba, the San'in Shiba, the Mino Shiba, the Akita Shiba (Shiba-Inu Preservation Association at

Omagari in Akita Prefecture) and the Ryukyu; nine Japanese local populations: Tanegashima, Yakushima, Amamioshima, Okinawahonto (middle and south regions), Iriomotejima, Mie hunting dogs at Shima peninsula, Mie hunting dogs at Nanto-machi, Iki and Tsushima; a Korean breed: the Jindo (pedigreed) and a population: Chejudo; Taiwan native dogs; Bangladesh native dogs; three Chinese origin dog breeds (pedigreed): the Chin, the Pug, and the Chow Chow; the Eskimo dog; Siberian breeds (pedigreed): the Middle Asian Sheepdog originating from Middle Asian in CIS and the Laika; and 43 European dog breeds (pedigreed): the Pointer, the Maltese, the Boxer, the German Shepherd, the Shetland Sheepdog, the Collie, the Beagle, the Pomeranian, the Poodle, the Doberman Pinscher, the Duckshund, the Yorkshire Terrier, the Dalmatian, the Cocker Spaniel, the English Setter and others. The name of dog breeds and populations and size of the samples are given in Table 1.

Horizontal starch gel electrophoresis (Smithies 1955, for enzymatic proteins), horizontal polyacrylamide gradient gel electrophoresis (Gahne et al. 1977 for non-enzymatic proteins), and thin layer chromatography (Hashimoto et al. 1984 for ganglioside monoxygenase).

Variations of blood proteins were observed in 14 loci including 9 isozymes: plasma eserine resistant esterase (*Es*), plasma leucine aminopeptidase (*Lap*), plasma alkaline phosphatase (*Akp*), erythrocyte hemoglobin (*Hb*), erythrocyte esterase-2 (*Es-2*), erythrocyte acid phosphatase (*Pac*), erythrocyte tetrazolium oxydase (*To*), erythrocyte glucose phosphate isomerase (*GPI*) and ganglioside monoxygenase (*Gmo*), and 5 proteins: plasma prealbumin-1 (*Pa-1*), plasma albumin (*Alb*), plasma postalbumin (*Poa*), plasma postalbumin-3 (*Poa-3*), and plasma transferrin (*Tf*), whereas 11 loci, including 8 isozymes: plasma esterase-fast (*Es-f*), plasma amylase (*Amy*), erythrocyte esterase-fast (*Cell-Es-f*), erythrocyte glucose-6-phosphate dehydrogenase (*G6PD*), erythrocyte adenyl kinase (*Ak*), erythrocyte leucine aminopeptidase (*Cell-Lap*) and erythrocyte lactate dehydrogenase-A and -B (*LDH-A* and *LDH-B*); and 3 proteins: plasma prealbumin-2 (*Pa-2*), plasma postalbumin-2 (*Poa-2*) and plasma slow- α_2 macroglobulin (α_2), were not variable. The previous studies (See TANABE, 1990, for references) revealed that the phenotypic variation of *Es*, *Lap*, *Akp*, *Hb*, *Es-2*, *Pac*, *To*, *GPI*, *Gmo*, *Pa-1*, *Alb*, *Poa*, *Poa-3*, and *Tf* are controlled, respectively, by the autosomal loci of *Es* with three codominant alleles, *Es^A*, *Es^B* and *Es^C*; *Lap* with two codominant alleles *Lap^A* and *Lap^B*; *Akp* with three codominant alleles, *Akp^A*, *Akp^B* and *Akp^C*; *Hb* with two codominant alleles, *Hb^A* and *Hb^B*; *Es-2* with a dominant allele, *Es-2^S* and a recessive allele, *Es-2^F*; *Pac* with two codominant alleles, *Pac^F* and *Pac^S*; *To* with two codominant alleles, *To^A* and *To^B*; *GPI* with two codominant alleles, *GPI^A* and *GPI^B*; *Gmo* with a dominant allele, *Gmo^S* and a recessive allele, *Gmo^a*; *Pa-1* with two codominant alleles, *Pa-1^A* and *Pa-1^B*; *Alb* with two codominant alleles, *Alb^F* and *Alb^S*; *Poa* with three codominant alleles, *Poa^A*, *Poa^B* and *Poa^C*; *Poa-3* with two codominant alleles, *Poa-3^A* and *Poa-3^B*; and *Tf* with five codominant alleles, *Tf^A*, *Tf^B*, *Tf^C*, *Tf^D* and *Tf^E*.

Table 1. Breed and number of the dogs used in this study

Breed or population	No. of dogs	Breed or population	No. of dogs
Hokkaido dog	119	Poodle	16
Akita dog	240	Doberman Pinscher	20
Kai dog	108	Collie	22
Kishu dog	81	Dachshund	18
Shikoku dog	90	Yorkshire Terrier	28
Shiba dog (San'in)	65	Dalmatian	14
(Shinshu)	206	Cocker Spaniel	20
(Mino)	113	English Setter	19
(Akita)	76	Middle-Asian Sheepdog	24
Tanegashima dogs	45	Eskimo dog	20
Yakushima dogs	38	Laika	8
Amamioshima dogs	92	Bulldog	6
(North)	71	Wire Haired Fox Terrier	6
(South)	21	Great Dane	6
Okinawahonto dogs	71	Borzoi	5
Iriomotejima dogs	20	Afghan Hound	5
Mie hunting dogs (Shima)	30	Labrador Retriever	4
(Nanto)	19	Saint Bernard	4
Iki dogs	40	Miniture Pinscher	4
Tsushima dogs	83	Old English Sheepdog	4
Ryukyu dog	30	Cairn Terrier	4
Mongrels in Japan	198	West Highland White Terrier	4
Korean native dogs	354	Scottish Terrier	4
(Jindo)	229	Irish Setter	3
(Chejudo)	125	Boston Terrier	3
Mongrels in Chejudo	4	Chihuahua	2
Taiwan native dogs	144	Cavalier King Charles Spaniel	2
(Atyal)	63	Golden Retriever	2
(Bunun)	27	Schnauzer	2
(Rukai)	34	Griffon Brixellios	2
(Ami)	20	Brittany Spaniel	1
Mongrels in Taiwan	44	Miniture Schnauzer	1
Bangladesh native dogs	60	Pyrenean Mountaindog	1
Sarail dogs in Bangladesh	4	Mastiff	1
Chin	27	Wire Haired Scotish Terrier	1
Pug	18	Basset Hound	1
Chow Chow	10	Japanese Terrier	1
Shi Tzu	9	Weimaraner	1
Pointer	64	Airdale Terrier	1
Maltese	73	Tosa dog	1
Boxer	26	Miniture Dachshund	1
German Shepherd	79	Bichon Frise	1
Shetland Sheepdog	33		
Beagle	412	Total breeds or populations	80
Pomeranian	27	Total number of the dogs	3445

Phylogeny of Asian breeds with emphasis on Japanese breeds

Our previous studies showed a distinct difference between Japanese native dog breeds and European dog breeds (Tanabe et al. 1977, 1978; SUGIURA et al. 1977; Tanabe, 1980). Later we demonstrated the gene flows from the Korean peninsula into the Japanese main islands except Hokkaido (Hashimoto et al., 1984; Tanabe et al. 1991; Tanabe, 1990, 1991). The most prominent differences of gene frequency among the dog breeds or populations were observed in *Hb* and *Gmo* variations. *Hb^A* was found only in Asian breeds or populations, but not in European breeds including Middle-Asian Sheepdog and Laika (Siberian breeds). *Hb* alleles among the Asian breeds or populations are shown in Figure 1. This data clearly show the gene flow of *Hb^A* from the Korean peninsula into the Japanese islands. A similar tendency was found in the genes of *Gmo*. *Gmo^S* was also found only in Asian breeds or populations, but not in European breeds including Middle-Asian Sheepdog and Laika. *Gmo* alleles among the Asian breeds or populations are shown in Figure 2. This Figure also shows the gene flow of *Gmo^S* from the Korean peninsula into Japanese island except Hokkaido.

GPI^A is a predominant allele in European breeds, but the frequency of *GPI^B* is higher in most of Asian breeds or populations than European breeds. *GPI* alleles among Asian breeds or populations are shown in Figure 3. This Figure also shows the gene flow of *GPI^A* from the Korean peninsula into the Japanese islands except northern parts.

Pa-3^A is a predominant allele in European breeds, but the frequency of *Pa-3^B* is higher in Asian breeds or populations than European breeds. *Poa-3* alleles among Asian breeds or populations are shown in Figure 4. This Figure also shows the gene flow of *Pa-3^B* from the Korean peninsula into all of the Japanese islands. Similar tendencies were observed the gene frequencies in *Poa*, *Alb*, *Tf*, *Es*, *Es-2* and *Pac* polymorphisms among the dog breeds or populations examined in this study.

Mean genetic distance between the dog breeds was calculated by the method of Nei (1975) using the data of 14 polymorphic and 11 monomorphic loci. From the matrix of genetic distance values, the dendrograms of the dog breeds were drawn by the unweighed pair-group method of clustering in numerical taxonomy (Sokal and Sneath, 1963) (Fig. 5).

For more clarifying the genetic positions of dog breeds or populations, a scatter diagram of the dog breeds in Z (1)-Z (2) planes was drawn from principal component analysis of the variance-covariance matrix of gene frequencies at 14 polymorphic loci. Phylogenetic relationship among 30 dog breeds defined by the first two (Z1-Z2) principal components of the distance calculated from variance-covariance matrix (methodology reference: Namikawa et al., 1984) is illustrated in Figure 6.

Figure 6 clearly shows the existence of the two close relationships among Taiwan native dogs, Chinese origin breeds (the Chin, the Pug and the Chow Chow) and some Japanese breeds (the Hokkaido, the Ryukyu, the Kai and the Mino-Shiba), and a close relationship among Korean native breed (the Jindo) or population (Chejudo), and most of Japanese native breeds or populations in Honshu and Shikoku. It can be postulated that there were two waves of the gene flow in dogs into Japan: the first was from southeast Asia through Taiwan and Ryukyu to whole of the Japanese islands, and the second from the Korean peninsula to the Japanese main islands except Hokkaido.

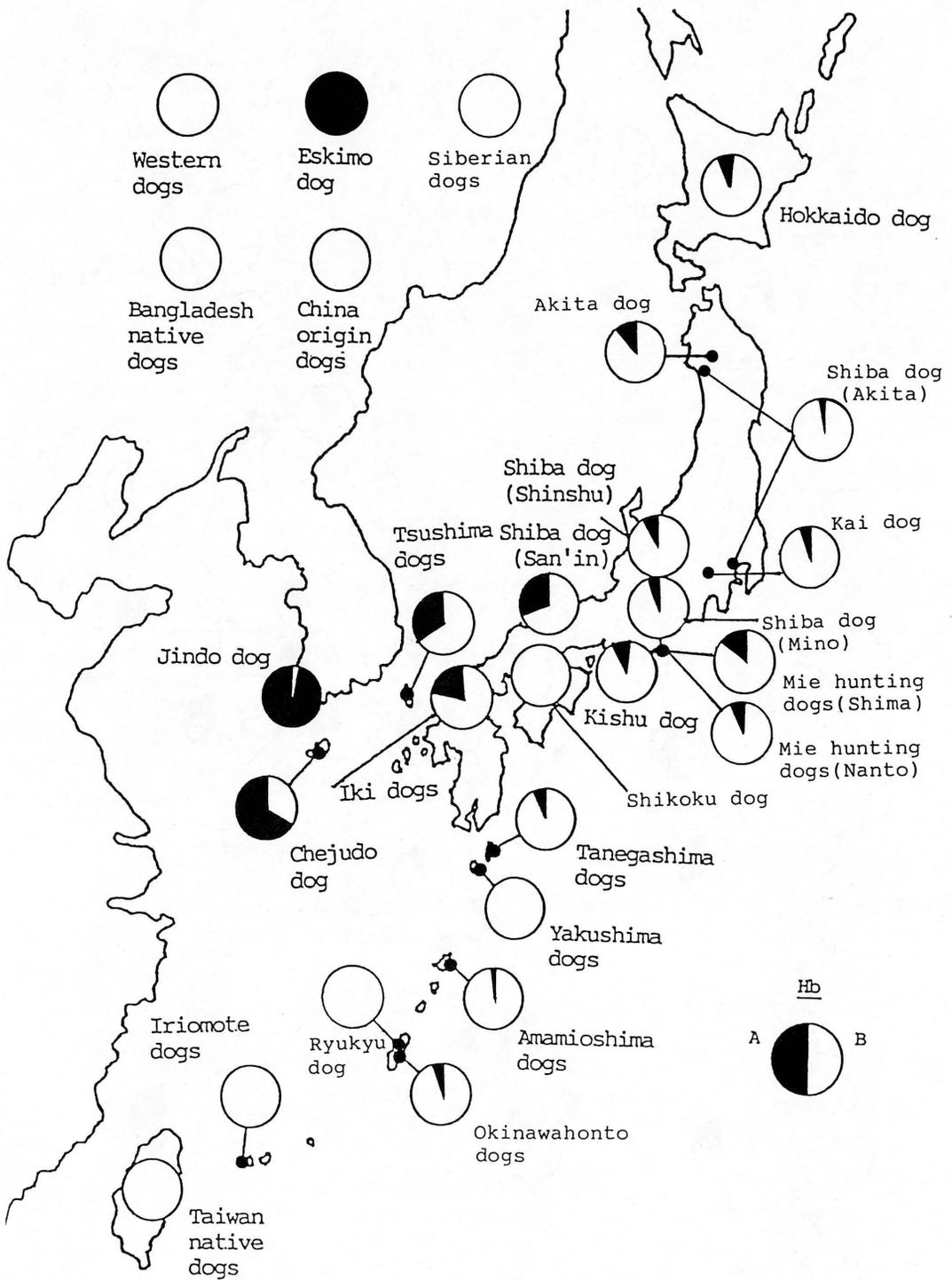


Fig.1. Distribution of canine erythrocyte hemoglobin (*Hb*) variants.

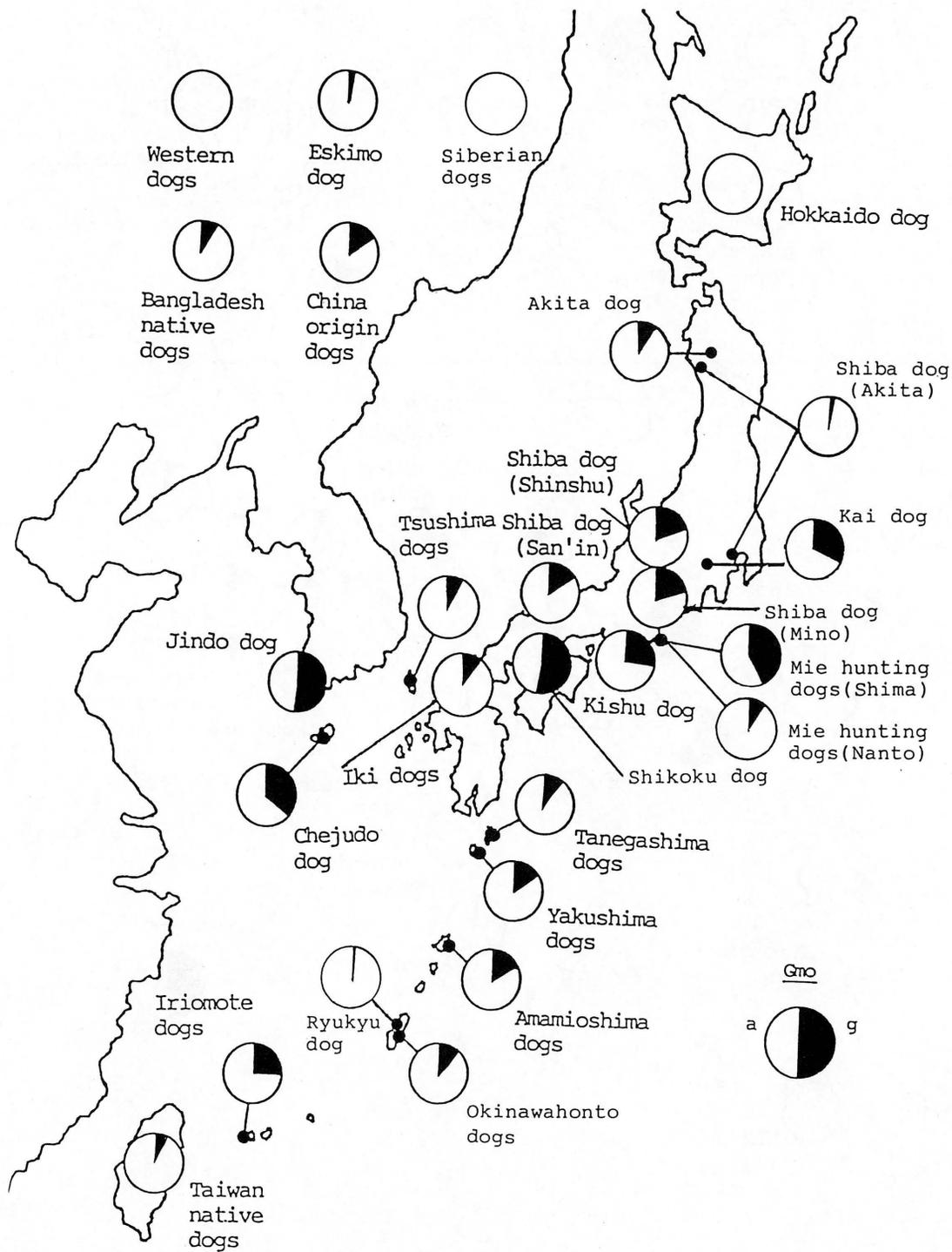


Fig.2. Distribution of canine erythrocyte ganglioside monoxygenase (*Gmo*) variants.

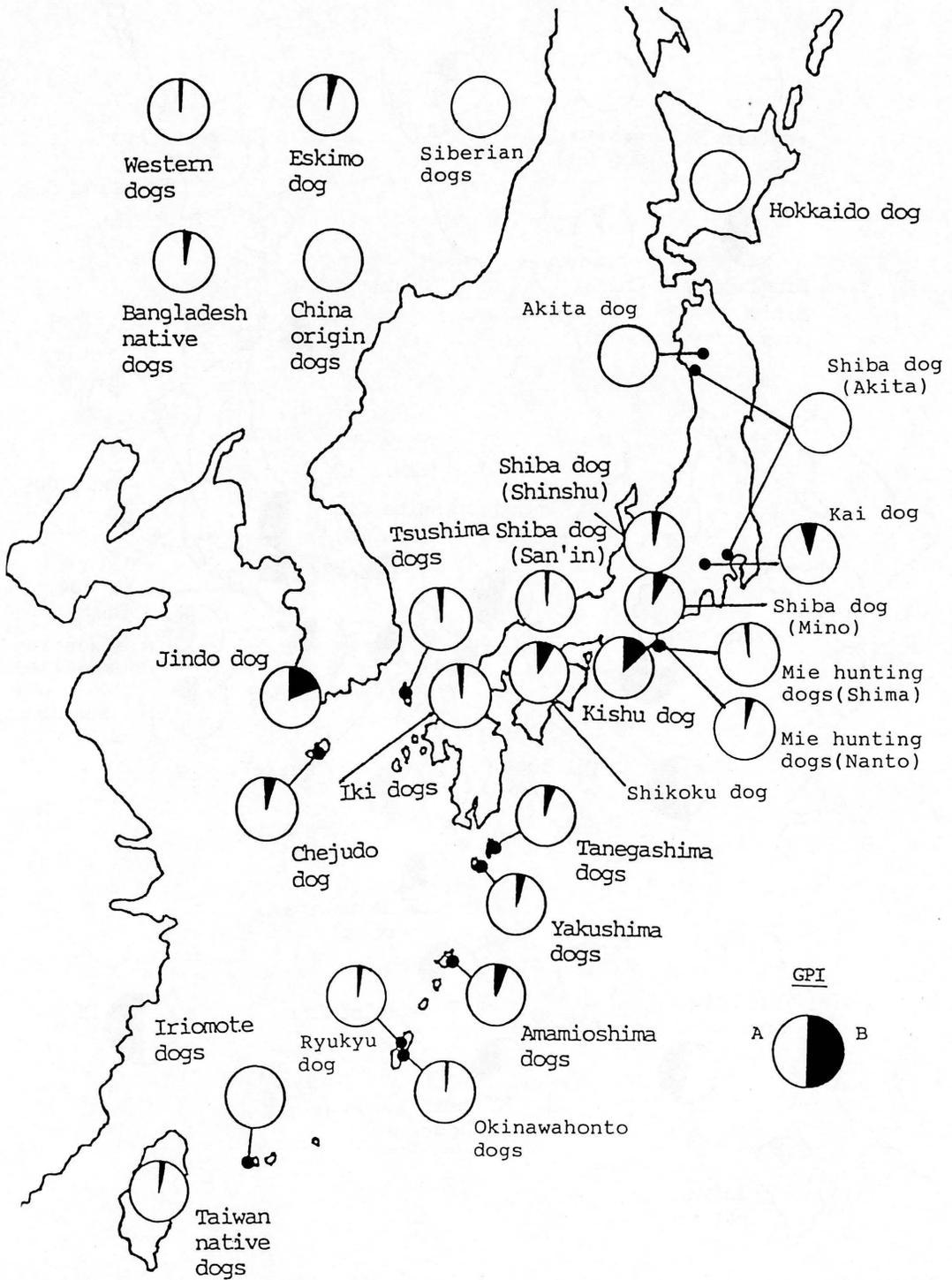


Fig.3. Distribution of canine erythrocyte glucose phosphate isomerase (GPI) variants.

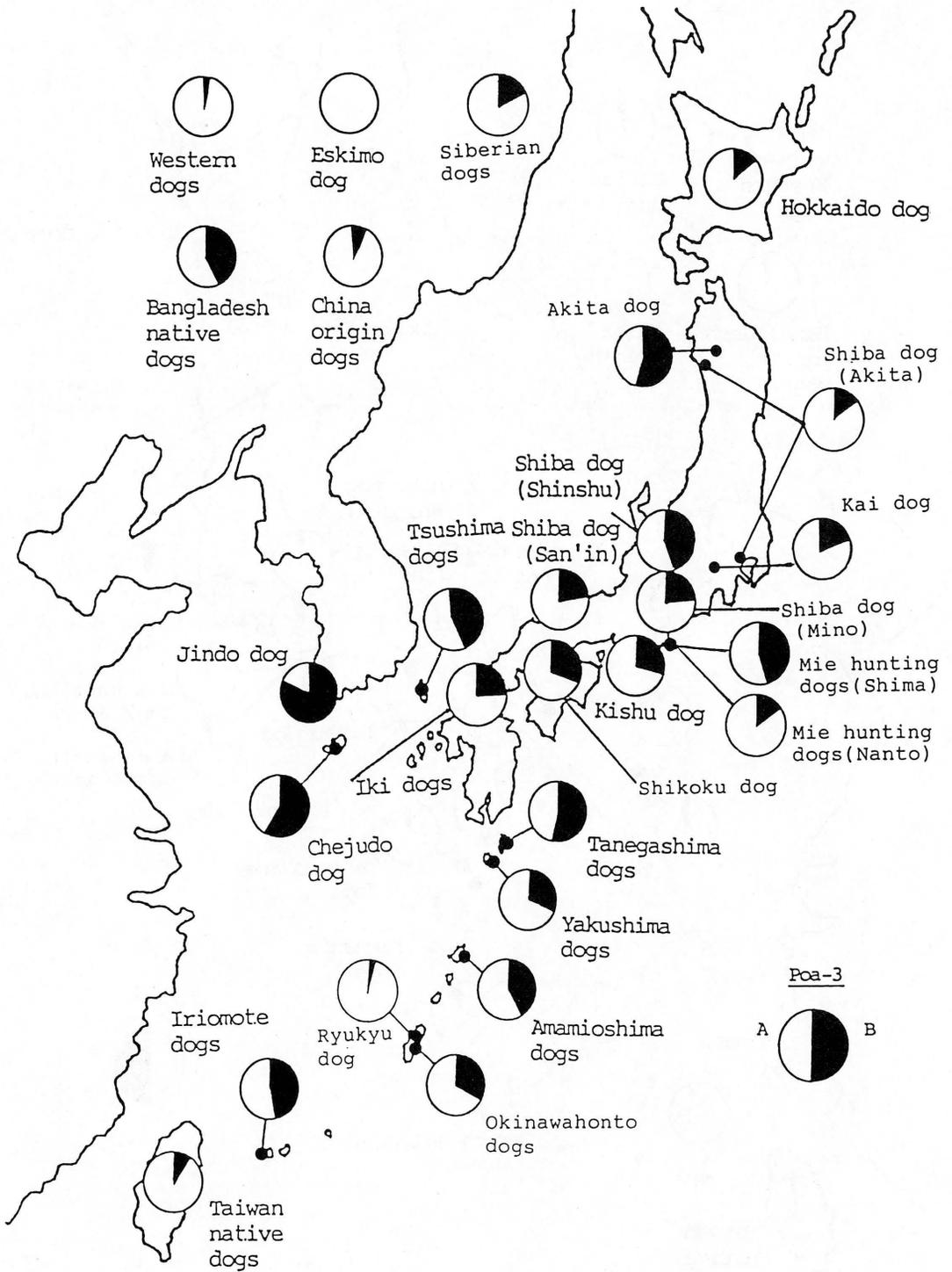


Fig.4. Distribution of canine plasma postalbumin-3 (*Poa-3*) variants.

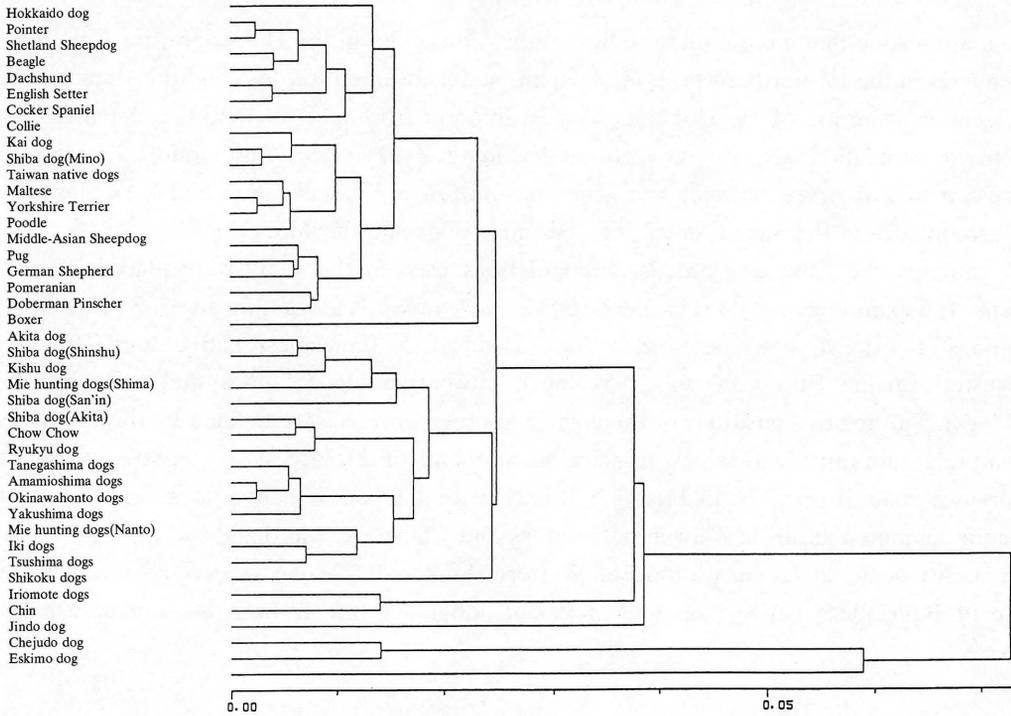


Fig.5. Dendrogram showing phylogenetic relationship among 43 dog breeds (Nei,UPG method).

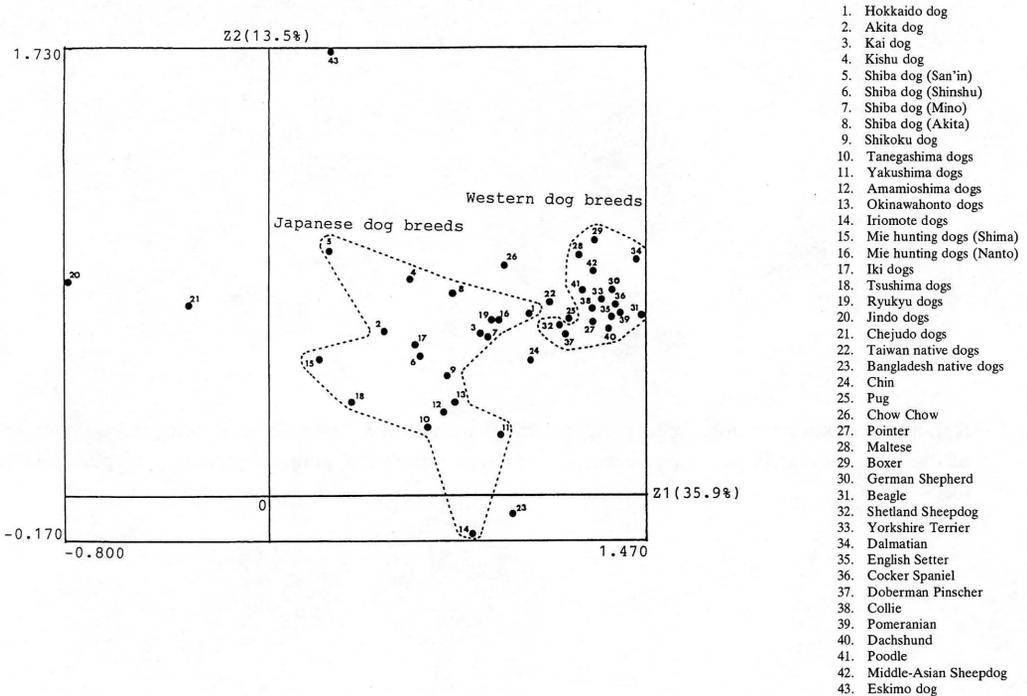


Fig.6. Relative position of 43 dog breeds defined by the first (Z1) and the second (Z2) largest principal components of the distance matrix based on variance-covariance analysis of gene frequency at 14 polymorphic loci.

It is interesting that a close relationship also was observed in the Hokkaido (the Ainu dog), which lives in the far-northern portion of Japan, and Taiwan native dogs and the Ryukyu dog. The gene constitution of the Hokkaido dog is different from most of the other Japanese dog breeds or populations except some groups including Ryukyu dog. Furthermore, a close relationship was observed between the gene constitution of Chejudo dogs and some Japanese dog groups such as the San'in Shiba dog, Tsushima dogs and the Akita dog.

To simplify the data, dog breeds or populations used in the study were placed in seven groups: 1. Japanese native dogs (1,556 dogs), 2. Korean native dogs (354 dogs), 3. Taiwan native dogs (144 dogs), 4. Chinese-origin dogs (64 dogs), 5. Bangladesh native dogs (60 dogs), 6. Western (mainly European) dogs (951 dogs), 7. Siberian dogs (32 dogs) and 8. Eskimo dog (20 dogs). The relative positions of the eight dog breed groups were defined by the first (Z1), second (Z2) and third (Z3) largest principal components of distance matrix based on variance-covariance analysis (Fig. 7). In Figure 7, it is clear that Japanese native dogs are located between a combined group of Taiwan native dogs and Chinese-origin dogs, and a group of Korean native dogs, while the position of Western dogs and Siberian dogs is nearer, whereas those of Bangladesh native dogs and of Eskimo dogs are farther from the Japanese native dogs.

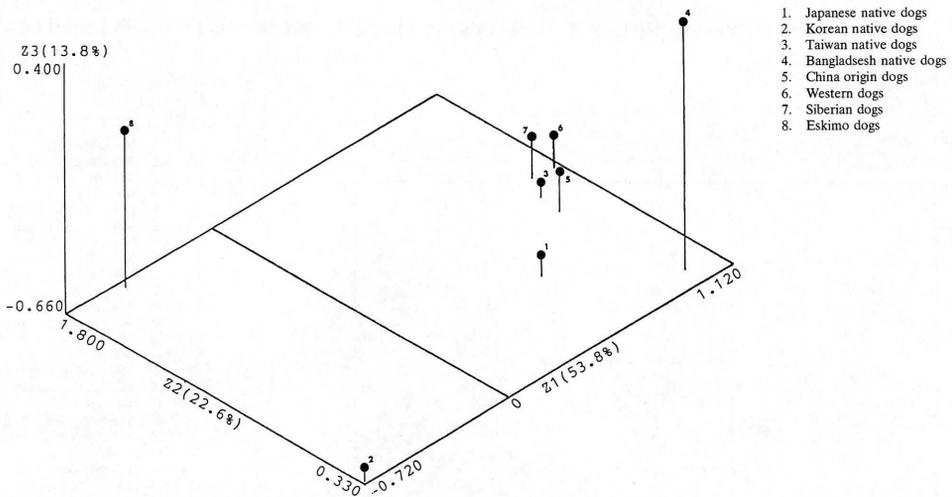


Fig.7. Relative position of 8 dog breed groups defined by the first three (Z1-Z3) principal components of the distance matrix based on variance-covariance analysis of gene frequency at 14 polymorphic loci.

An assumption of the migration routes of Japanese dogs

From the results described above, it is postulated that the Hokkaido (Ainu) breed is a descendant of an old type of Japanese dog which was brought 10,000-12,000 years ago to Japan by Jomonese who came from Southeast Asia. The other Japanese native breeds are descendants of the hybrid between the old type of Japanese dogs and Korean origin dogs which were brought 1,700-2,300 years ago by Yayoi migrants who came through the Korean peninsula.

The cranial studies on fossil dogs of Japan and Korea support the hypothesis on the migration routes of dogs stated above. Dog skulls found in Kuwanae remains in Oita Prefecture, Kyushu (aging ca. 2,000 years, the middle Yayoi period) having deep stops (Nishihara 1989) showed a close affinity to dog skulls found in Uenongigiseoripohang remains in north Korea (aging 2,500-3,000 years), also having deep stops (Kim 1973), and were quite different from dog skulls found in many shell-mounds of the Jomon period (2,300-10,000 years ago), the skulls of the dog having very shallow or flat stops (Shigebara 1989).

By human cranial studies, Hanihara (1984, 1991) showed the close affinities among Ainu, Okinawans and Jomonese. Omoto (1972, 1984) reported that the genes controlling ear wax and blood protein polymorphisms of the present Japanese people including the Ainu and the people in adjacent areas in Asia, show similarities between the Ainu and people living in southeast Asia, and between the Japanese living in Honshu and the Koreans.

The wild mice in the north Japan (Hokkaido and northern-half of Tohoku district) are close in the restriction of their mitochondrial DNA to those of southeast Asia including Taiwan, and those of middle and southeast Japan (Honshu except northern-half of Tohoku district, Shikoku and Kyushu) are close those of northeast Asia (Korea, Siberia and north China) (Yonekawa et al., 1988). The distribution pattern of mtDNA sequences is almost the same as in the case of Japanese dogs. Yonekawa et al (1988) concluded that the wild mice from southeast Asia distributed first in Japan, and then another variety of mice came from northeast Asia in accompany with new human groups who migrated through the Korean peninsula, and distributed in middle and southwest of Japan.

All the data on the dogs described in this paper fairly clarify the ancestry of the Japanese native dogs, and also enable us to assume the ancestry of the Japanese people who brought the ancestors of the Japanese native dogs.

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日本犬の系統に関する研究、特に日本犬の渡来ルートについて、
田名部雄一

日本を含む、アジアおよびヨーロッパ犬品種や集団の系統を、電気泳動法やクロマトグラフィーで検出される血液蛋白質の多型を指標として調べた。

分析に用いた血液は日本犬7品種4系統（北海道犬、秋田犬、甲斐犬、柴犬4系統、紀州犬、四国犬、琉球犬）、韓国犬1品種（珍島犬）、中国原産犬3品種（チン、パグ、チャウチャウ）、エスキモー犬、ヨーロッパ犬15品種（ポインター、マルチーズ、ボクサー、ジャーマンシェパード、ビーグル、シェトランドシープドッグ、ヨークシャテリア、ダルメシアン、イングリッシュセッター、コッカスパニエル、ドーベルマンピンシェル、コリー、ポメラニアン、ダックスフンド、プードル）、シベリア犬2品種（中央アジアシープドッグ、ライカ）、および日本在来犬9集団（種子島、屋久島、奄美大島、沖縄本島—中南部、西表島、三重実猟犬2群—志摩半島および南島町、壱岐、対馬）、韓国在来犬1集団（済州島犬）、台湾在来犬1集団（高山地方犬）、バンラディッシュ在来犬1集団の合計3,445頭から採血した。蛋白質多型現象は血漿エステラーゼ、血漿ロイシンアミノペプチダーゼ、血球ヘモグロビン、血球エステラーゼ2、血球酸性ホスファターゼ、血球グルコースホスフェイトイソメラーゼ、血球テトラゾリウムオキシダーゼ、血球ガングリオシドモノオキシゲナーゼ、血漿プレアルブミン1、血漿アルブミン、血漿ポストアルブミン3および血漿トランスフェリンの合計14種の蛋白質に認められた。これらはいずれもそれぞれの遺伝子座上の遺伝子により支配されている。

上述した43の犬品種又は集団について、これら多型の認められた遺伝子座の遺伝子頻度の差を、主成分分析を行い、その品種又は集団の遺伝的遠近関係を散布図として示した。これから、台湾在来犬、中国原産犬、および日本犬種中北海道犬（アイヌ犬）、琉球犬の相互間に近い関係が認められ、また韓国犬品種（珍島犬）と同集団（済州島犬）と本州、四国にいる大部分の日本犬、品種や集団の相互間にも近い関係が認められた。

このことは、日本犬の成立に2つの遺伝子の流れがあったことを示している。その一つは東南アジアからのもので、恐らく台湾琉球を経て、日本列島全体に入った。もう一つは朝鮮半島を経て、北海道や琉球の一部を除く大部分の日本列島に入ったものである。このことから、北海道犬（アイヌ犬）は古い犬の子孫であり、この古い犬は1万年から1万2千年前に縄文人が東南アジアから持ち込んだものと推定された。大部分の他の日本犬は（琉球犬や南西諸島の一部の犬を除く）この古い犬と弥生人が1,700年から2,300年前に朝鮮半島から渡来して持ち込んだ、新しい犬との雑種の子孫であると推定された。