CHAPTER 5

DISCUSSION

Discussion

The biochemical polymorphism of blood enzymes and serum proteins in goats had been investigated earlier by many workers utilizing the methods of zone and horizontal electrophoresis in starch and acrylamide (Khanolkar *et al.*, 1963; Bernhardt, 1964; Watanabe and Suzuki, 1965; Efremov and Braend, 1965; Osterhoff and Ward-Cox, 1970; Ordermatt 1973; Nishida *et al.*, 1975 ; Schoeman, 1977; Nozawa *et al.*, 1978 a,b; Tucker *et al.*, 1980 , 1983 & 1989; Katsumata *et al.*, 1981 a,b; Fesus *et al.*, 1983; Barbancho *et al.*, 1984; Shotake. *et al.*, 1986., Bhat,1986 &1987; Tunon *et al.*, 1987 a,b & 1989; Osterhoff *et al.*,1987; Wang *et al.*,1991; Vankan and Bell,1992; Stasio *et al.*,1993 & 1995; Pepin and Nguyen,1994; Ma Ning *et al.*,1996).

Since cellulose acetate electrophoresis is the method of first choice in this study, attempts were made to develop methodologies for analysing blood enzyme and proteins on this medium. No existing methodology was available from literature for analysing goat biochemical markers using cellulose acetate electrophoresis except for one recent work from Nigeria by Ologun and Imumorni (1996).Their work was only on one locus which is haemoglobin. However, cellulose acetate electrophoresis methods employed for analysis of samples (red cells and plasma) were adopted as a first step towards establishing the methodologies. As a guideline to develop the methodologies, many references pertaining to cellogel electrophoresis was followed. Once the methods developed, the cellulose acetate electrophoresis was employed for the analysis of all the genetic markers in this study except X-protein where starch gel electrophoresis was employed.

The phenotypic and allelic frequencies which have been obtained for the forty biochemical markers in the native goats of Southeast Asia, Sri Lanka and Australia in this study are assessed in relation to the results obtained by these workers and others who have studied various breeds of goats in Southeast Asia and elsewhere.

It is only appropriate to mention here again that in the present study goat blood samples except the Australian feral goat (crossbred population) samples were collected only from 'katjang type' (native dwarf) goats and not from any exotic or crossbred populations. Australian Feral goats may also be considered as Australian native goats, although not in the strict. sense. These goats were imported long ago from various countries and have adapted to the Australian environment. Therefore it would be appropriate to mention them as indigenous or native. Similar studies conducted by earlier workers from the same region are based on samples from either crossbreds, exotic or even native breeds but of a smaller size.

5.1 Albumin

Two albumin types have been described earlier for the plasma albumin of domestic goats, although two different nomenclatures have been used widely. These are Alb^{A} and Alb^{B} alleles, Alb^{A} being more anodal (Watanabe and Suzuki, 1967; Osterhoff and Ward-Cox, 1970) and Alb^{F} and Alb^{S} (Salerno et al., 1968; Tjankov, 1972; Tunon *et al.*, 1989). The former nomenclature has been used in this study (Table 31).

Two albumin alleles namely Alb^{A} and Alb^{B}, were found in this study. The locus did show some genetic variability although the Alb^{A} allele appeared in high frequency (> 0.70) in all the populations. In Musuan, Hat Yai and Hambantota, the frequency was lower. This finding is in line with results obtained by Tunon *et al.*, (1989) in 14 Spanish breed of goats, where they reported great genetic variability and gene

frequency of allele Alb^A fluctuated from 0.17 to 0.97. In this study the gene frequency of allele Alb^A ranged only from 0.615 (Hat Yai) to 0.952 (Thambuthegama).

Studies conducted in South Africa by Osterhoff *et al.*, (1987) was found to be even more contrasting. They detected high frequencies for allele Alb^B (0.98) in Angora goats and monomorphism for allele Alb^B in Boer, Saanen and the natives goats. Similar results differing from the present study was also observed in the study conducted by Barbancho *et al.*, (1984) in three of the four Spanish breeds whose frequencies of allele Alb^B is considerably higher then Alb^A except in the Serrana Andaluza goat breed. A summary of gene frequencies of albumin obtained by various authors from various breeds of goats are listed in Table 31. In many of the other studies, the non-detection of polymorphism for albumin has been reported in the native goats of Norway (Efremov and Braend, 1965), India (Singh *et al.*, 1977), Korea (Katsumata *et al.*, 1982), Sri Lanka (Shotake et al., 1986) and in Hungary (Fesus *et al.*, 1983), although in Sri Lankan numbers involved in the study were small.

Therefore, it can be pointed out that the Spanish breeds maintained a higher genetic variability for this marker (albumin) in comparison with goat population in this study. However, it would seem from this study that Alb^A is fixed in the Southeast Asian and Australian goat populations where frequency ranges from 0.62 to 0.95 (Table 32).

Populations from Ujung Pandang and to a lesser extent from Musuan were not in Hardy-Weinberg equilibrium and this might have been caused by one or more of the following factors: assortive mating, selection and genetic drift. Factors such as these and/or combination of them are most significant especially with sampling done in small-holder farms in villages.

Table 31. Summary of gene frequencies of albumin from various breeds of goats.

Breeds /or Locality	(No)	Alb ^{A}	Alb ^{B}	Reference
Japan				
Japanese Saanen	(686)	0.96	0.04	Watanabe and Suzuki, 1967
Japanese native goats	(506)	0.75	0.25	Watanabe and Suzuki, 1967
Swiss Saanen	(39)	No polymorphism		Watanabe and Suzuki, 1967
German coloured goats	(81)	0.29	0.71	Watanabe and Suzuki, 1967
Italian Alpine	(45)	0.17	0.83	Watanabe and Suzuki, 1967
Hungarian Saanen	(39)	0.80	0.20	Watanabe and Suzuki, 1967
Luciana (South Italy)	(100)	0.34	0.65	Salerno *et al.*, 1968
Okinawa goats	(225)	No polymorphism		Nozawa *et al.*, 1986
Japanese Saanen	(71)	-	1.00	Nozawa *et al.*, 1986
Japanese Saanen	(245)	No polymorphism		Katsumata *et al.*, 1981b
Korean native goats	(190)	No polymorphism		Katsumata *et al.*, 1981b
Indonesia				
Etawah	(40)	0.08	0.82	Katsumata *et al.*, 1981b
Katjang	(32)	0.47	0.53	Katsumata *et al.*, 1981b
Local	(33)	0.24	0.76	Katsumata *et al.*, 1981b
Spanish breeds				
Grandina	(80)	0.270	0.730	Barbancho *et al.*, 1984
Murciana	(113)	0.354	0.646	Barbancho *et al.*, 1984
Malaguena	(96)	0.281	0.719	Barbancho *et al.*, 1984
Serrana Andaluza	(110)	0.723	0.277	Barbancho *et al.*, 1984
Sri Lanka				
Native goats	(21)	No polymorphism		Nozawa *et al.*, 1986
South Africa				
Boer	(241)	-	1.00	Osterhoff *et al.*, 1987
Native	(219)	-	1.00	Osterhoff *et al.*, 1987
Saanen	(150)	-	1.00	Osterhoff *et al.*, 1987
Angora	(150)	0.02	0.98	Osterhoff *et al.*, 1987

(Contd)

Table 31. Summary of gene frequencies of albumin from various breeds of goats

Breeds /or Locality	(No)	Alb ^{A}	Alb ^{B}	Reference
Spanish breeds				
Pirenaica	(115)	0.55	0.45	Tunon *et al.*, 1989
Verata	(100)	0.44	0.56	Tunon *et. al*, 1989
Guadarrama	(101)	0.91	0.09	Tunon *et* al., 1989
Zamorana	(100)	0.76	0.244	Tunon *et al.*, 1989
Berciana	(101)	0.51	0.49	Tunon *et al.*, 1989
Granadina	(100)	0.24	0.76	Tunon *et. al*, 1989
Blanca Andaluza	(100)	0.57	0.434	Tunon *et al.*, 1989
Murciana	(100)	0.17	0.83	Tunon *et al.*, 1989
Negra Serrana	(100)	0.58	0.42	Tunon *et al.*, 1989
Malaguena	(100)	0.31	0.69	Tunon *et al*, 1989
Canaria	(99)	0.20	0.80	Tunon *et al.*, 1989
Palmera	(36)	0.43	0.57	Tunon *et al.*, 1989
Retinta	(108)	0.99	0.01	Tunon *et al.*, 1989

Table 32. Gene frequencies of albumin from the present study

Breeds /Locality	(No)	Alb ^{A}	Alb ^{B}
Malaysia			
MARDI/IPSR	(55)	0.93	0.07
Sabah	(51)	0.80	0.20
Sarawak	(71)	0.78	0.22
Indonesia			
Bogor	(50)	0.76	0.24
Ujung Pandang	(48)	0.72	0.28
Medan	(51)	0.97	0.21
Philippines			
Musuan	(51)	0.67	0.33
Thailand			
Chengmai	(50)	0.75	0.25
Hat yai	(39)	0.62	0.38
Sri Lanka			
Hambantota	(10)	0.65	0.35
Weerawilla	(37)	0.91	0.09
Thambuthegama	(31)	0.95	0.05
Australia			
New South Wales	(52)	0.89	0.11

5.2. Amylase

Polymorphism in goat amylase locus was first reported by Fechter and Pretorius (1970). Later Osterhoff and Ward-Cox (1970) described two alleles and three phenotypes. These reports were confirmed in Jamnapari and Barbari goats by Bhat and Baruah (1980). They delineated two genes *Amy* ^{1} (*Amy* ^{A}) and *Amy* ^{II} (*Amy* ^{B}), the later being at a low frequency in these two breeds. A summary of the gene frequencies of amylase obtained by various authors from various breeds of goats are listed in Table 33.

Unlike two distinctly separated bands in starch gel electrophoresis employed by many authors, in cellulose acetate electrophoresis, two phenotypes of same electrophoretic mobility were observed, *Amy* ^{H} (strongly stained band) and Amy L (weakly stained band), their genetic control being due to autosomal alleles , *Amy* ^{H} and *Amy* ^{L}, with dominance of *Amy* ^{H}. This study did not reveal much differences in the overall gene frequency data for the locus, but there is a tendency for the allele Amy L (> 0.05) to predominate in most of the goat populations except in Sabah (0.48) and New South Wales (0.44) as shown in Table 34..

The allele *Amy* ^{A} is practically fixed for all the breeds studied so far with high frequencies of *Amy* ^{A} and even its fixing is a common feature, as the frequencies for that allele estimated by various authors, were never lower than 0.90 (Fechter and Pretorius, 1970; Osterhoff and Ward-Cox, 1970; Nozawa *et al.*, 1978b; Barbancho *et al.*, 1980; Fesus *et al.*, 1983 and Tunon *et al.*, 1989) except in one study, 0.80 (Shotake *et al.*, 1986).

The nature of the genes controlling the alleles *Amy* ^{A} and *Amy* ^{B} in many studies, and *Amy* ^{H} and *Amy* ^{L} in this study are yet to be determined fully. However, when plasma

Table 33. Summary of frequencies of amylase from various breeds of goats

Breeds /or Locality	(No)	Amy ^{A}	Amy ^{B}	Reference
Braune and Weisse Deutsche Edelziege	67	1.000	-	Meyer (1967)
Angora	85	0.964	0.036	Fechter& Pretorius (1970)
South African goats				
Boer	212	1.000	-	Osterhoff & Ward-Cox
Angora, aborters	87	1.000	-	(1972)
Angora, non-aborters	110	0.900	0.100	"
Toggenburg	19	1.000		Tjankov (1970)
Indigenous (Bulgaria)	24	1.000		Tjankov (1970)
Appenzeller	105	1.000		Kunz (1974)
Verzasca	118	1.000		Kunz (1974)
Walliser Schwarzhals	122	1.000		Kunz (1974)
Japanese native goats				
Iheyajima	41	0.940	0.060	Nozawa *et al.*, (1978)
Izenanajima	25	0.940	0.060	Nozawa *et al.*, (1978)
North Okinawa	16	0.960	0.040	Nozawa *et al.*, (1978)
Agunijima	51	0.990	0.010	Nozawa *et al.*, (1978)
Zamanijima	28	0.940	0.060	Nozawa *et al.*, (1978)
Vonagunijima	27	1.000	-	Nozawa *et al.*, (1978)
South Daitojima	28	1.000	-	Nozawa *et al.*, (1978)
Japanese Saanen	71	0.990	0.010	Nozawa *et al.*, (1978)
Jamnapari (India)	98	0.995	0.050	Bhat & Baruah (1980)
Barbari (India)	52	0.980	0.020	Bhat & Baruah (1980)
Hungarian native goat	224	0.996	0.004	Fesus *et al.*, (1983)
Sri Lanka goats				
University of Peradeniya	5	1.000	-	Shotake *et al.*, 1986
Galle	36	1.000	-	Shotake *et al.*, 1986
Negembo	10	0.800	0.200	Shotake *et al.*, 1986
Hambantota	30	1.000	-	Shotake *et al.*, 1986
Sigiriya	36	1.000	-	Shotake *et al.*, 1986

(Contd)

Table 33. Summary of frequencies of amylase from various breeds of goats

Breeds / or Locality	(No)	Amy ^{A}	Amy ^{B}	Reference
Spanish breeds				
Pirenaica	115	-	1.000	Tunon *et al.*, 1989
Verata	100	-	1.000	Tunon *et al.*, 1989
Guadarrama	101	-	1.000	Tunon *et al.*, 1989
Zamorana	110	-	1.000	Tunon *et al.*, 1989
Berciana	100	-	1.000	Tunon *et al.*, 1989
Granadina	101	-	1.000	Tunon *et al.*, 1989
Blanca Andaluza	100		1.000	Tunon *et al.*, 1989
Blanca Celtiberica	110	-	1.000	Tunon *et al.*, 1989
Murciana	100	-	1.000	Tunon *et al.*, 1989
Negra Serrana	100	-	1.000	Tunon *et al.*, 1989
Malaguena	100	-	1.000	Tunon *et al.*, 1989
Canaria	99	-	1.000	Tunon *et al.*, 1989
Palmera	36	-	1.000	Tunon *et al.*, 1989
Retinta	108	-	1.000	Tunon *et al.*, 1989

Table 34. Frequencies of amylase from the present study

Breeds /Locality	(No)	Amy ^{H}	Amy ^{L}
Malaysia			
MARDI/IPSR	(55)	0.409	0.591
Sabah	(51)	0.520	0.480
Sarawak	(71)	0.394	0.606
Indonesia			
Bogor	(50)	0.320	0.680
Ujung Pandang	(48)	0.427	0.573
Medan	(51)	0.380	0.620
Philippines			
Musuan	(51)	0.333	0.667
Thailand			
Chengmai	(50)	0.420	0.580
Hat yai	(39)	0.397	0.603
Sri Lanka			
Hambantota	(10)	0.500	0.500
Weerawilla	(37)	0.378	0.662
Thambuthegama	(31)	0.435	0.565
Australia			
New South Wales	(52)	0.558	0.442

samples were subjected to both cellulose acetate and starch gel electrophoresis, no relationship what so ever was established between the two genes. These preliminary studies do indicate that there are separate genes controlling those alleles.

5.3 Alkaline phosphatase

Lode (1970) reported existence of genetic control for individual variation in serum alkaline phosphatase in goats. Two phenotypes of Ap were found: Ap F and Ap O. their genetic control being due to two autosomal alleles, Ap^F and Ap^O, with dominance of Ap^F (Suzuki and Watanabe, 1968). Summary of the gene frequencies for the various breeds of goats studied are listed in Table 35.

Considerable differences exist in the gene frequency values of this system among the thirteen goat populations studied (Table 36). Similar types of alkaline phosphatase have been demonstrated in Angora (Tsunoda *et al.*, 1976), Jamnapari, Black Bengal and Barbari (Bhat and Baruah, 1980), Barbari and Beetal goats (Joshi and Singh), 1980), Spanish breeds (Tunon *et, al.*, 1989), Sri Lankan native goats (Shotake *et al.*, 1986) and Japanese native goats (Nozawa *et al.*, 1987b).

In accordance to this study the occurrence of the allele Ap^O seems to predominate (frequency > 0.53) but in Hat Yai and Weerawilla goat populations, the frequency was lower (<0.49) as shown in Table 36. This phenomenon does not agree with the results obtained so far among the Sri Lankan native goats (Shotake *et al.*, 1986) and the Japanese native goats (Nozawa *et al.*, 1978b) where there is a predominance of the allele Ap^F (frequency > 0.70).

Table 35. Summary of frequencies of Alkaline phosphatase from various goat breeds.

Breeds /or Locality	(No)	Ap^F	Ap^O	Reference
Japanese native goats				
Iheyajima	(41)	0.87	0.1333	Nozawa *et al.*, (1978)
Izenajima	(25)	0.96	0.04	Nozawa *et al.*, (1978)
North Okinawa	(16)	0.93	0.07	Nozawa *et al.*, (1978)
Agunijima	(51)	0.89	0.11	Nozawa *et al.*, (1978)
Zamanijima	(28)	0.86	0.141	Nozawa *et al.*, (1978)
Vonagunijima	(27)	0.90	0.10	Nozawa *et al.*, (1978)
South Daitojima	(28)	0.92	0.08	Nozawa *et al.*, (1978)
Japanese Saanen	(71)	0.71	0.29	Nozawa *et al.*, (1978)
Sri Lanka native goats				
University of Peradeniya	(5)	1.0	-	Shotake *et al.*, 1986
Galle	(36)	1.000	-	Shotake *et al.*, 1986
Negembo	(10)	0.80	0.200	Shotake *et al.*, 1986
Hambantota	(30)	1.00	-	Shotake *et al.*, 1986
Sigiriya	(36)	1.00	-	Shotake *et al.*, 1986
Spanish breeds				
Pirenaica	(115)	0.66	0.3343	Tunon et al., 1989
Verata	(100)	0.21	0.79	Tunon et al., 1989
Guadarrama	(101)	0.20	0.80	Tunon et al., 1989
Zamorana	(110)	0.12	0.85	Tunon et al., 1989
Berciana	(100)	0.49	0.51	Tunon et al., 1989
Granadina	(101)	0.19	0.81	Tunon et al., 1989
Blanca Andaluza	(100)	0.37	0.63	Tunon et al., 1989
Blanca Celtiberica	(110)	0.12	0.88	Tunon et al., 1989
Murciana	(100)	0.11	0.89	Tunon et al., 1989
Negra Serrana	(100)	0.19	0.81	Tunon et al., 1989
Malaguena	(100)	0.10	0.90	Tunon et al., 1989
Canaria	(99)	0.14	0.86	Tunon et al., 1989
Palmera	(36)	0.09	0.91	Tunon et al., 1989
Retinta	(108)	0.48	0.52	Tunon et al., 1989

Table 36. Frequencies of Alkaline phosphatase from the present study.

Breeds /Locality	(No)	Ap^F	Ap^O
Malaysia			
MARDI/IPSR	(55)	0.46	0.54
Sabah	(51)	0.42	0.58
Sarawak	(71)	0.29	0.71
Indonesia			
Bogor	(50)	0.47	0.53
Ujung Pandang	(48)	0.25	0.75
Medan	(51)	0.31	0.69
Philippines			
Musuan	(51)	0.26	0.74
Thailand			
Chengmai	(50)	0.45	0.55
Hat yai	(39)	0.53	0.47
Sri Lanka			
Hambantota	(10)	0.45	0.55
Weerawilla	(37)	0.51	0.48
Thambuthegama	(31)	0.44	0.56
Australia			
New South Wales	(52)	0.4446	0.54

It should, nevertheless be pointed out that in the various studies conducted so far, there is a tendency for high frequencies for allele Ap^{F}, especially the Spanish Pirenaica (0.66), Sri Lankan Negembo native goats (0.80) and Japanese native goats (>0.70) and on the other hand there is also high frequency for allele Ap^{O}, especially the Spanish Palmera (0.91), Spanish Malaguena (0.90) and in the Sarawak native goats (0.71). In none of the breeds/or populations studies is there a clear tendency towards the fixing of either of the alleles of Alp.

5.4 Carbonic anhydrase

Prior to this study, no report of polymorphism for carbonic anhydrase in goats was observed (Tucker & Clarke, 1980; Fesus *et al.*, 1983; Tucker *et al.*, 1983; Hasima, 1986 and Tunon *et, al.*, 1987b) as shown in Table 37.

Five phenotypes were observed in red cell carbonic anhydrase in this study : Ca 102/102, Ca 102/100, Ca 100/100, Ca 100/98 and Ca 98/98. The three commonest phenotypes observed, Ca 100/100, Ca 100/98, and Ca 98/98 have been identified in almost all the populations and the rarest phenotypes were Ca 102/102 and Ca 102/100. They are all attributed to three common alleles: Ca^{102}, Ca^{100} and Ca^{98} in homozygous and heterozygous combinations. Carbonic anhydrase shows differences among population, but the Ca^{100} allele was the most common in all populations (Table 38).

The frequency of most common allele Ca^{100} was found to be substantially high in all populations ranging from 0.533 (Bogor and Ujung Pandang) to 0.978 (New South Wales). The rarest allele Ca^{102} was only found in the goat population of Weerawilla but in low frequency (0.028).

Table 37. Summary of frequencies of Carbonic anhydrase from various goat breeds

Breeds /or Locality	(No)	Ca^F	Ca^S	References
Great Britain				
Saanen	(122)		No variation	Tucker *et al.*, 1983
South Africa				
Local goats	(168)		No variation	Tucker *et al.*, 1983
Boer	(48)		No variation	Tucker *et al.*, 1983
Angora	(7)		No variation	Tucker *et al.*, 1983
Saanen	(10)		No variation	Tucker *et al.*, 1983
Cross-bred	(32)		No variation	Tucker *et al.*, 1983
Spanish breeds				
Pirenaica	(115)	-	1.00	Tunon *et al.*, 1989
Verata	(100)	-	1.00	Tunon *et al.*, 1989
Guadarrama	(101)	-	1.00	Tunon *et al.*, 1989
Zamorana	(110)	-	1.00	Tunon *et al.*, 1989
Berciana	(100)	-	1.00	Tunon *et al.*, 1989
Granadina	(101)	-	1.00	Tunon *et al.*, 1989
Blanca Andaluza	(100)	-	1.00	Tunon *et al.*, 1989
Blanca Celtiberica	(110)	-	1.00	Tunon *et al.*, 1989
Murciana	(100)	-	1.00	Tunon *et al.*, 1989
Negra Serrana	(100)	-	1.00	Tunon *et al.*, 1989
Malaguena	(100)	-	1.00	Tunon *et al.*, 1989
Canaria	(99)	-	1.00	Tunon *et al.*, 1989
Palmera	(36)	-	1.00	Tunon *et al.*, 1989
Retinta	(108)	-	1.00	Tunon *et al.*, 1989

Table 38. Frequencies of Carbonic anhydrase from the present study.

Breeds /Locality	(No)	Ca ^{102}	Ca ^{100}	Ca ^{98}
Malaysia				
MARDI/IPSR	(53)	0.000	0.887	0.113
Sabah	(51)	0.000	0.920	0.080
Sarawak	(71)	0.000	0.977	0.023
Indonesia				
Bogor	(50)	0.000	0.533	0.467
Ujung Pandang	(48)	0.000	0.533	0.467
Medan	(50)	0.000	0.880	0.120
Philippines				
Musuan	(51)	0.000	0.849	0.151
Thailand				
Chengmai	(50)	0.000	0.849	0.151
Hat yai	(39)	0.000	0.974	0.026
Sri Lanka				
Hambantota	(10)	0.100	0.974	0.026
Weerawilla	(37)	0.028	0.944	0.028
Thambuthegama	(31)	0.000	0.935	0.065
Australia				
New South Wales	(52)	0.000	0.978	0.022

With greater differences observed in the gene frequency values, this genetic system maintains a high degree of variability in the Southeast Asia , Sri Lankan and Australian goat populations.

Difference in selection pressures posed by a variety of environmental conditions, or due to differences in the degree of inbreeding may also be the causes for significant difference ($p<0.05$) for the genotype populations.

5.5. Haemoglobin

Polymorphism in goat haemoglobin was first reported by Harris and Warren (1955). Goat haemoglobin is a tetramer consisting of 2 alpha and 2 beta globin chains plus one haem group per chain. Five different Hbs (Hb A, Hb B, Hb O, Hb D Malta and Hb E) have been described in adult non-anemic goats (Huisman, 1970; Bannister *et al*, 1979). Hb A and Hb B are alpha chain variants and the others are beta chain variants. Gene frequencies obtained by others in various breeds of goats studied (Table 39) indicated that the Hb^A allele predominates or is fixed, so that the Hb A phenotype occurs in high frequencies. Watanabe *et al.*, (1965) reported an exception to this phenomenon in Hungarian Saanen and Italian goats.

Out of thirteen native goat populations in the present study, nine populations (MARDI/IPSR, Sabah, Sarawak, Bogor, Ujung Pandang, Medan, Musuan., Chengmai and Hat Yai) show a high incidence of Hb A phenotype compared to Hb B. Exception were only observed in four populations (Hambantota, Weerawilla, Thambuthegama and New South Wales) which showed higher incidence for gene frequency of allele Hb^B (Table 40).

The three Malaysian goat populations revealed a less intense but distinct band which appears in advance of Hb A band and is temporarily designated as Hb A^X. This was also reported by Hasima (1986) in here while working with the Malaysian goats, using starch gel electrophoresis. However, the presence of Hb A^X in these populations were very small.

In an endeavor to identify the Hb A^X band, various possibilities can be eliminated. Hb A^X cannot be a forward band of Hb B since it appears in advance of Hb A. Hb D has a slower mobility than Hb B (Adams *et at.*, 1983), but those tested were all above 6 months in age. Hb E cannot be distinguished by cellulose acetate electrophoresis, but Tucker *et al.*, (1983) has showed that Hb E has a slightly slower electrophoretic mobility than Hb A.

Hasima (1986) pointed out that Hb A^X band could be possibly **Hb C**. However from this study point of view it cannot be Hb C which replaces Hb F in the early month of life, because the goats concerned were all adults. Although samples were only collected from healthy animals, the possibility that these animals may be anaemic, cannot however be excluded. The remaining alternative is that this Hb A^X band could be a new alpha or beta chain variant, and hence a new phenotype .

In order to ascertain this, various biochemical and genetic methods of investigation must be carried out which includes chromatography studies of the structure of alpha and beta chain, and progeny testing to establish the inheritance of these blood proteins. Unfortunately, this was established for all the animals tested as the pedigree samples did not have the Hb A^XA phenotype. Crosses between goats with this phenotype to determine whether it is a true phenotype controlled by a particular allele has yet to be

Table 39. Summary of frequencies of Haemoglobin from various breeds of goat

Breeds /or Locality	(No)	Hb^A	Hb^B	References
Braune Deutsche Edelziege	(150)	0.927	0.073	Bernhardt (1964)
Weisse Deutsche Edelziege	(100)	0.980	0.020	Bernhardt (1964)
Native Norwegian goat	(108)	No polymorphism		Efremov & Braend 1965
Japanese Saanen	(1177)	0.915	0.085	Watanabe *et al.*, (1965)
Tokara	(15)	0.966	0.034	Watanabe *et al.*, (1965)
Tokara & its hybrids	(554)	0.979	0.021	Watanabe *et al.*, (1965)
German coloured	(54)	0.882	0.118	Watanabe *et al.*, (1965)
Italian Alpine	(49)	0.404	0.596	Watanabe *et al.*, (1965)
Hungarian Saanen	(56)	0.462	0.538	Watanabe *et al.*, (1965)
Swiss Saanen	(56)	1.000	-	Watanabe *et al.*, (1965)
South African goats				
African Boer	(212)	0.91	0.09	Osterhoff& Ward-Cox (1970)
Indigenous	(7)	0.95	0.05	Osterhoff& Ward-Cox (1970)
Angora, aborters	(110)	0.93	0.07	Osterhoff& Ward-Cox (1970)
Angora, non aborters	(147)	0.94	0.06	Osterhoff&Ward-Cox (1970)
Toggenburg	(134)	0.951	0.049	Odermatt (1973)
Bunder-strahlenziege	(127)	1.00	-	Odermatt (1973)
Appenzeller	(105)	0.981	0.019	Kunz, (1974)
Verrzasca	(118)	1.00	-	Kunz, (1974)
Walliser Schwarzhals	(122)	1.00	-	Kunz, (1974)
Indian goat	(116)	0.965	0.035	Naik (1975)
Katjang goat - P. Malaysia	(28)	No polymorphism		Nishida *et al.*, (1975)
Katjang goat - E. Malaysia	(54)	No polymorphism		Nishida *et al.*, (1975)
Indian goats				
Jamnapari	(70)	1.00	-	Joshi *et al.*, (1975)
Barbari	(76)	0.93344	0.066	Joshi *et al.*, (1975)
Barbari	(38)	1.00	-	Singh *et al.*, (1977)
Beetal	(89)	1.00	-	Singh *et al.*, (1977)
Jamnapari	(98)	1.00	-	Baruah & Bhat *et al.*, (1980)
Black-Bengal	(81)	1.00	-	Baruah & Bhat *et al.*, (1980)
Barbari	(180)	0.98	0.020	Bhat *et al.*, (1983)
Jamnapari	(89)	1.00	-	Bhat *et al.*, (1983)
Malaysian goats				
Anglo-Nubian	(12)	1.00	-	Jothi (1981)
British-Alpine	(11)	0.955	0.045	Jothi (1981)
Saanen	(15)	0.634	0.366	Jothi (1981)
Feral goat	(19)	0.869	0.131	Jothi (1981)
Katjang goat	(25)	0.860	0.140	Jothi (1981)

(Contd)

Table 39. Summary of frequencies of Haemoglobin from various breeds of goat

Breeds /or Locality	(No)	Hb^A	Hb^B	$Hb\ A^X$	References
Hungarian native goat	(224)	0.954	0.046		Fesus *et al.*, (1983)
South Africa					
Boer	(268)	0.998	0.002		Schoeman, (1977)
Native	(387)	0.950	0.050		Tucker *et al.*, 1983
Saanen	(164)	0.740	0.260		Tucker *et al.*, 1983
Angora	(152)	1.000	-		Tucker *et al.*, 1983
Spanish breeds					
Granadina	(80)	0.846	0.154		Barbancho *et al.*, (1984)
Murciana	(133)	0.932	0.068		Barbancho *et al.*, (1984)
Malaguena	(96)	0.844	0.156		Barbancho *et al.*, (1984)
Serrana Andalaza	(10)	0.927	0.073		Barbancho *et al.*, (1984)
Malaysian Katjang goats					
University of Malaya	(56)	0.964	0.036	-	Hasima (1986)
Kuala Selangor	(61)	0.943	0.025	0.032	Hasima (1986)
MARDI	(128)	0.008	0.097		Hasima (1986)
Spanish breeds					
Pirenaica	(115)	0.980	0.020		Tunon *et al.*, (1989)
Verata	(100)	0.720	0.280		Tunon *et al.*, (1989)
Guadarrama	(101)	1.000	-		Tunon *et al.*, (1989)
Zamorana	(110)	0.990	0.010		Tunon *et al.*, (1989)
Berciana	(100)	0.960	0.040		Tunon *et al.*, (1989)
Granadina	(101)	0.890	0.110		Tunon *et al.*, (1989)
Blanca Andaluza	(100)	1.000	-		Tunon *et al.*, (1989)
Blanca Celtiberica	(110)	0.790	0.210		Tunon *et al.*, (1989)
Murciana	(100)	0.980	0.020		Tunon *et al.*, (1989)
Negra Serrana	(100)	0.980	0.020		Tunon *et al.*, (1989)
Malaguena	(100)	0.830	0.170		Tunon *et al.*, (1989)
Canaria	(99)	0.800	0.200		Tunon *et al.*, (1989)
Palmera	(36)	0.940	0.060		Tunon *et al.*, (1989)
Retinta	(108)	1.000	-		Tunon *et al.*, (1989)

Table 40. Frequencies of haemoglobin from the present study.

Breeds /Locality	(No)	Hb^A	Hb^B	Hb A^X
Malaysia				
MARDI/IPT	(55)	0.891	0.045	0.064
Sabah	(51)	0.873	0.059	0.069
Sarawak	(71)	0.923	-	0.077
Indonesia				
Bogor	(50)	0.960	0.040	-
Ujung Pandang	(48)	0.813	0.188	-
Medan	(50)	0.900	0.100	
Philippines				
Musuan	(51)	0.824	0.176	-
Thailand				
Chengmai	(50)	0.840	0.160	-
Hat yai	(39)	0.897	0.103	
Sri Lanka				
Hambantota	(10)	0.150	0.850	-
Weerawilla	(37)	0.278	0.722	-
Thambuthegama	*(31)*	*0.113*	*0.887*	-
Australia				
New South Wales	(52)	0.2231	0.769	-

carried out. Until a proper re-evaluation of the present nomenclature is done, the present nomenclature of Hb A^X will be used.

In the present study, the three Sri Lanka goat populations and the Australian goat population had highest frequency of phenotype Hb B. The Hb B is probably the most favoured phenotype in these locations as Australian Feral and Sri Lankan goats are populations with mixed descent. Whereas, the allele Hb^A was more predominant in all the other nine goat populations studied.

5.6. Malic enzyme

The first report on erythrocyte malic enzyme was from Manwell and Baker (1977), who described two variants migrating faster than F and S variants of sheep. Rasero *et al.*, (1989) described the presence of a third variant found in two Italian goat populations reared in Sicily, Derivata di Siria and Maltase. The three observed variants, called A, B and C are in order of decreasing electrophoretic mobility.

From studies conducted by Rasero *et al.*, (1989), about 70% of the goat populations observed highest frequency for the allele Me^B, while Me^A was more frequent in Maltase (20%) and Me^C in Derivata di Siria 24%). Assuming that only one locus is involved, six observed phenotypes are known to be controlled by three codominant alleles, called Me^A, Me^B and Me^C. In both the studies of Manwell and Baker (1977) and Rasero *et al.*, (1989), no family studies were conducted to confirm the genetic basis of different phenotypes.

In the present study, four variants were observed: Me 104, Me 102, Me 100 and Me 98 in order of decreasing electrophoretic mobility. No reference sample is available, but it is supposed that Me 102, Me 100 and Me 98 variants correspond to those already described by Rasero *et al.*, (1989) i.e. Me A = Me 102, Me B = Me 100 and Me C = Me

98. The variant Me 104 was only observed in 2 individuals of New South Wales goat population. The three common phenotypes Me 102, Me 102/100 and Me 100 have been identified in all the goat populations. They are attributed to the two common alleles: Me^{100} and Me^{102}, in homozygous and heterozygous combinations. The rare alleles are Me^{104} and Me^{98}.

Family studies conducted (Table 12) showed that the observed phenotypes of the offspring were consistent with the hypothesis that Me phenotypes observed are coded for by an autosomal locus with three codominant alleles. No pedigree samples with phenotypes Me 104 was available, hence further investigation on the polymorphism of malic enzyme and the mode of inheritance are needed before confirming the inheritance of the variant Me 104 (the fourth codominant allele).

There is no significant difference ($P>0.05$) in the allelic frequencies among the various goat populations. Me^{100} was found to be the most common allele, in all the populations except New South Wales, the range being 0.350 (Hambantota) to 0.882 (MARDI/IPSR). The frequency of Me^{98} is consistently low ranging from 0.029 (New South Wales) to 0.319 (Weerawilla). In the New South Wales goat population Me^{102} was known to be higher than allele Me^{100}. In the Hambantota goat population both the allele Me^{102} and Me^{100} have the same gene frequency (0.350).

The absence of allele Me^{98} in the MARDI/IPSR goat population could be explained using the Founder principal (Ford, 1964). It is applied when a few individuals from a large population are isolated (in this case, selected and kept in the nucleus herd) and the alleles borne through these founders are subsequently not represented in the same frequency as that of the original populations. It is known that the original MARDI/IPSR goat population was founded through the purchase of few animals from various villages.

5.7. Malate dehydrogenase

The only report on Malate dehydrogenase polymorphism by Shotake *et al.*, (1986) was confirmed by studies on the Sri Lankan native goats. The allele Mdh^{1} had significantly higher frequency (0.986) compared to allele Mdh^{2} (0.014). Apart from this study, no other reports on goat malate dehydrogenase polymorphism is available as shown in Table 41.

Three distinct phenotypes were observed, the two homozygous types i.e. the faster Mdh 100 and slower Mdh 98 and the heterozygous phenotype Mdh 100/98. From the family studies conducted, the Mdh phenotypes were found to be controlled by two autosomal alleles Mdh^{100} and Mdh^{98} (Table 13). As there is no reference sample available, the fast homozygous type Mdh^{100} (the most commonest allele) could correspond to Mdh 1 (the most commonest allele) as reported by Shotake *et al.*, (1986).

Results from the study (Table 42) also indicated that the allele Mdh^{100} seems to be the most common allele among all the populations, except Hambantota with allelic frequency ranging from 0.542 (Weerawilla) to 0.903 (Thambuthegama). In the Hambantota goat population the allele frequency of Mdh^{98} (0.550) was slightly higher than allele Mdh^{100} (0.450). The Mdh^{100} allele in this study was more prevalent just like the faster allele Mdh^{1} of Shotake *et al.*, (1986). This blood system showed considerable amount of genetic variability.

Only the goat population of Hambantota were in Hardy-Weinberg equilibrium. The rest of the populations may have had the adverse effects of the factors that cause inequilibrium such as inbreeding, assortative mating and natural selection .

Table 41. Summary of Gene frequency of Malate dehydrogenase from various breeds of goats.

Breeds /or Locality	No	Mdh^1	Mdh^2	References
Jamnapari	(10)	No variation		Nishida *et al.*, (1975)
Japanese native goats	(225)	No variation		Nozawa *et al.*, (1978)
Malaysian goats				
Anglo Nubian	(12)	No variation		Jothi, (1981)
British Alpine	(11)	No variation		Jothi, (1981)
Saanen	(8)	No variation		Jothi, (1981)
Feral goats	(9)	No variation		Jothi, (1981)
Katjang goat	(25)	No variation		Jothi, (1981)
Sri Lanka native goats				
Uni. of Peradeniya	(15)	0.850	0.150	Shotake *et al.*, (1986)
Galle	(30)	1.000	0.000	Shotake *et al.*, (1986)
Negambo	(10)	0.776	0.224	Shotake *et al.*, (1986)
Hambantota	(30)	1.000	0.000	Shotake *et al.*, (1986)
Sigiriya	(36)	0.920	0.080	Shotake *et al.*, (1986)
Spanish breed	No variation observed			Tunon *et al.*, (1987b)

Table 42. Gene frequencies of Malate dehydrogenase from the present study

Breeds /Locality	(No)	Mdh^{100}	Mdh^{98}
Malaysia			
MARDI/IPT	(55)	0.755	0.245
Sabah	(51)	0.647	0.353
Sarawak	(71)	0.732	0.268
Indonesia			
Bogor	(50)	0.790	0.210
Ujung Pandang	(48)	0.656	0.344
Medan	(50)	0.770	0.230
Philippines			
Musuan	(51)	0.735	0.265
Thailand			
Chengmai	(50)	0.720	0.280
Hat yai	(39)	0.526	0.474
Sri Lanka			
Hambantota	(10)	0.450	0.550
Weerawilla	(36)	0.542	0.458
Thambuthegama	(31)	0.903	0.097
Australia			
New South Wales	(52)	0.827	0.173

5.8. Nucleoside phosphorylase

Nucleoside phosphorylase polymorphism has been indicated by Tucker *et. al.*, (1976) using starch gel electrophoresis and isoelectric focussing but the differentiation of phenotypes is not satisfactory to understand the mode of inheritance. No variations (Table 43) were observed in the various Spanish breeds of goats studied by Tunon *et al.*, (1987b).

However, in the present study two distinct bands observed were Np H (high activity) and Np L (low activity). Both these phenotypes were supported and confirmed by a spectrophotometric assay studies by Sekaran *et al.*, 1989. Family studies revealed that there are two allomorphic genes involved, one specifying for high activity and the other for low activity.

Significant difference exist in the gene frequency values for the allele Np^{L} among the different goat populations (Table 44) ranging from 0.435 to 0.712. However, the allele Np^{L} was found in higher frequency than allele Np^{H} in MARDI/IPSR, Sabah, Ujung Pandang, Musuan, Chengmai, Hambantota and New South Wales. In both the goat populations of Hat Yai and Weerawilla, the gene frequencies were the same. In none of the goat populations studied is there a clear tendency towards fixing of either of alleles of Np. This genetic system thus maintains a considerable degree of variability in the Southeast Asian and Australian goat populations.

Table 43. Summary of gene frequencies of nucleoside phosphorylase from various goat breeds

Breeds/or Locality	(No)	Np^H	Np^L	References
Spanish breeds				
Pirenaica	(115)	No variation observed		Tunon *et al.*, (1987b)
Verata	(100)	No variation observed		Tunon *et al.*, (1987b)
Guadarrama	(101)	No variation observed		Tunon *et al.*, (1987b)
Zamorana	(110)	No variation observed		Tunon *et al.*, (1987b)
Berciana	(100)	No variation observed		Tunon *et al.*, (1987b)
Granadina	(101)	No variation observed		Tunon *et al.*, (1987b)
Blanca Andaluza	(100)	No variation observed		Tunon *et al.*, (1987b)
Blanca Celtiberica	(110)	No variation observed		Tunon *et al.*, (1987b)
Murciana	(100)	No variation observed		Tunon *et al.*, (1987b)
Negra Serrana	(100)	No variation observed		Tunon *et al.*, (1987b)
Malaguena	(100)	No variation observed		Tunon *et al.*, (1987b)
Canaria	(99)	No variation observed		Tunon *et al.*, (1987b)
Palmera	(36)	No variation observed		Tunon *et al.*, (1987b)
Retinta	(108)	No variation observed		Tunon *et al.*, (1987b)

Table 44. Gene frequencies of nucleoside phosphorylase from the present study

Breeds / or Locality	(No)	Np^H	Np^L
Malaysia			
MARDI/IPSR	(55)	0.364	0.636
Sabah	(51)	0.480	0.520
Sarawak	(71)	0.528	0.472
Indonesia			
Bogor	(50)	0.530	0.470
Ujung Pandang	(48)	0.385	0.615
Medan	(50)	0.550	0.450
Philippines			
Musuan	(51)	0.333	0.667
Thailand			
Chengmai	(50)	0.430	0.570
Hat yai	(39)	0.500	0.500
Sri Lanka			
Hambantota	(10)	0.450	0.550
Weerawilla	(36)	0.550	0.550
Thambuthegama	(31)	0.565	0.435
Australia			
New South Wales	(52)	0.288	0.712

5.9. NADH-Diaphorase 1 zone 1

Tucker and Clarke (1980), while carrying out a comparative study involving the different genera and species of the Caprinae family, including hybrids, demonstrated the existence of two zones of diaphorase activity on starch gel electrophoresis in the domestic goat. The two zones are Dia 1 and Dia 2 in decreasing order of mobility. Later, Tunon and Gonzalez (1987a) also reported two zones of diaphorase activity corresponding to zones described by Tucker and Clarke (1980).

The two regions of diaphorase activity described by Tunon and Gonzalez (1987a) in region 2 consisted of a single band of activity in the most cathodal area of the starch gel. In region 1, one or two bands appear in a more anodal position than region 2. In some samples the band was relatively anodal in mobility (phenotype F), whereas in others there was a clearly more cathodal migration of the band (phenotype S) and in others there was a pair comprising each type of band (phenotype FS).

As mentioned earlier, both Tucker & Clarke (1980) and Tunon and Gonzalez (1987a) described two zones of diaphorase activity in decreasing order of mobility i.e. Dia 1 and Dia 2. In the present study, the two zones of diaphorase activity were described in increasing order of mobility i.e Dia 1 and Dia 2. . Hence, the nomenclature used in the present study Dia-1 probably corresponds to Dia -2 described by Tucker & Clarke (1980) and Tunon *et al.*, (1987a). This genetic system of blood has been shown to be monomorphic in a few goat populations so far studied (Nozawa *et al.*, 1978a, b; Katsumata *et al.*, 1981 a, b; Tucker & Clarke, 1980; Tunon *et al.*, 1987b).

In the present study, complete homozygosity for the locus was observed in MARDI/IPSR, Bogor, Ujung Pandang, Medan, Hambantota, Weerawilla, Thambuthegama and New South Wales. The occurrence of high degree of inbreeding have probably lead to the non-variable Dia-1 (Table 45).

The most common allele was found to be allele *Dia-1* ^{100} among all the populations ranging from 0.657 to 1.000. From the test carried out, three populations, Sarawak, Musuan and Chengmai were not in Hardy-Weinberg equilibrium. The Musuan samples have all the phenotypes probably because there was no selective pressure against any of four alleles in this locality.

Table 45. Gene frequencies of NADH-Dia -1 from the present study

Breeds / or Locality	(No)	102	100	98
Malaysia				
MARDI/IPT	(55)	-	1.000	-
Sabah	(51)	-	0.941	0.059
Sarawak	(71)	-	0.871	0.129
Indonesia				
Bogor	(50)	-	1.000	-
Ujung Pandang	(48)	-	1.000	-
Medan	(50)	-	1.000	-
Philippines				
Musuan	(49)	0.071	0.684	0.245
Thailand				
Chengmai	(50)	-	0.870	0.130
Hat yai	(39)	-	0.846	0.154
Sri Lanka				
Hambantota	(10)	-	1.000	-
Weerawilla	(36)	-	1.000	-
Thambuthegama	(31)	-	1.000	-
Australia				
New South Wales	(52)	-	1.000	-

5.10. NADH-Diaphorase 1 zone 2

Genetic polymorphism of NADH-Diaphorase in goats was first described by Tunon *et al.*, (1987a) in Spanish breeds of goats. Tucker and Clarke (1980), demonstrated the existence of two zones of Diaphorase activity, DIA 1 and DIA 2 in a comparative study involving the different gene and species of the Caprinae family, including hybrids in the domestic goat. No variation was observed.

Three phenotypes of Diaphorase were detected in the most anodic region of Dia 1: Dia F, Dia FS and Dia S, in decreasing order of mobility by Tunon *et al.*, (1987b). In 13 of the 14 breeds studied, the Diaphorase was shown to be polymorphic, allele Dia^{F} being the most common allele with frequency ranging from 0.822 to 1.00 (Table 46).

NADH-Diaphorase region 1 as described by Tunon *et al.*, (1987a,b) probably correspond to type 1 as described by Tucker and Clarke (1980). Although there is no reference samples , the NADH-Dia 1 zone 2, [Dia-2] in this present study, probably correspond to NADH-Dia region 1 described by Tucker and Clarke (1980) and Tunon *et al.*, (1987a). The Dia F, Dia FS and Dia S described by Tunon *et al.*, (1987a) correspond to Dia -2 102/102, Dia -2 102/100 and Dia -2 100/100 respectively observed in the study (Table 46).

Though few goat populations have been analyzed in the world for this system, it would seem strange that no variation was found in any of them (Ozawa *et al.*, 1978 a, b,; Katsumata *et al.*, 1981 a,b; 1982; Di Stasio *et al.*, 1984; Shotake *et al.*, 1986) except in the Spanish breed (Tunon *et al.*, 1987a). The present study however indicates polymorphism for almost all the goat populations studied (Table 47).

Populations from Sabah, Sarawak, Bogor, Ujung Pandang, Medan, Musuan, Chengmai, Thambuthegama and New South Wales were not in Hardy-Weinberg

Table 46. Summary of gene frequencies of NADH-Dia -1 from various breeds of goats

Breeds	(No)	Dia ^{F}	Dia ^{S}	Reference
Japanese native goats	(225)	No variation		Nozawa *et al.*, (1987b)
Japanese Saanen	(71)	No variation		Nozawa *et al.*, (1987b)
Japanese Saanen Breed	(245)	No variation		Katsumata *et al.*, (1981b)
Korean native goats	(190)	No variation		Katsumata *et al.*, (1982)
Malaysian Katjang goats	(82)	No variation		Nishida *et al.*, (1975)
Malaysian Saanen	(10)	No variation		Nishida *et al.*, (1975)
Sri Lankan native goats	(121)	No variation		Shotake *et al.*, (1986)
Spanish breeds				
Pirenaica	(115)	No variation		Tunon *et al.*, (1987a,b)
Verata	(100)	No variation		Tunon *et al.*, (1987a,b)
Guadarrama	(101)	No variation		Tunon *et al.*, (1987a,b)
Zamorana	(100)	No variation		Tunon *et al.*, (1987a,b)
Berciana	(101)	No variation		Tunon *et al.*, (1987a,b)
Granadina	(100)	No variation		Tunon *et al.*, (1987a,b)
Blanca Andaluza	(100)	No variation		Tunon *et al.*, (1987a,b)
Murciana	(100)	No variation		Tunon *et al.*, (1987a,b)
Negra Serrana	(100)	No variation		Tunon *et al.*, (1987a,b)
Malaguena	(100)	No variation		Tunon *et al.*, (1987a,b)
Canaria	(99)	No variation		Tunon *et al.*, (1987a,b)
Palmera	(36)	No variation		Tunon *et al.*, (1987a,b)
Retinta	(108)	No variation		Tunon *et al.*, (1987a,b)

Table 47. Gene frequencies of NADH-Dia -2 from the present study.

Breeds / or Locality	(No)	Dia-2	102	100	98
Malaysia					
MARDI/IPSR	(55)		0.018	0.973	0.009
Sabah	(49)		0.224	0.776	0.000
Sarawak	(62)		0.298	0.702	0.000
Indonesia					
Bogor	(50)		0.280	0.280	-
Ujung Pandang	(48)		0.135	0.865	-
Medan	(50)		0.100	0.900	-
Philippines					
Musuan	(49)		0.224	0.776	-
Thailand					
Chengmai	(50)		0.170	0.830	-
Hat yai	(39)		0.122	0.757	0.122
Sri Lanka					
Hambantota	(10)		-	1.000	-
Weerawilla	(36)		0.029	0.800	0.171
Thambuthegama	(31)		0.484	0.516	-
Australia					
New South Wales	(52)		0.721	0.279	-

equilibrium. In the Hambantota population, all the individuals were homozygous for the allele *Dia-2* ^{100}. This could be highly due to the increased level of inbreeding in this population. Another probability for the complete homozygosity for this locus could be due to occurrence of non random mating which increases the frequency of homozygotes. The Hat Yai and Weerawilla samples had all the phenotypes observed probably because there was no selective pressure against any of the four alleles.

5.11. Transferrin

Three phenotypes of ß-globulin were described by Aston and Mc Doughall (1958) and Millision and Patisson (1961) on starch gel electrophoresis. These ß-globulins were known as transferrin (Watanabe *et al.*, 1965).

The majority of the goat breeds studied to date show three phenotypes controlled by codominant alleles Tf^A and Tf^B, and showing a much higher frequency of Tf^A and Tf^B, the frequency of Tf^A being 0.7-1.0 (Watanabe and Suzuki, 1973; Tjankov, 1970; Fesus *et al.*, 1983; Barbancho *et al.*, 1984; Tunon *et al.*, 1987). Osterhoff and Ward-Cox (1970) described the presence of four alleles of transferrin: Tf^A, Tf^B, Tf^C and Tf^D. A summary of gene frequencies of transferrin obtained by various authors from various breeds of goats are listed in Table 48.

In the present study, four alleles of transferrin were detected: Tf^A, Tf^B, Tf^C and Tf^D, with eight phenotypes being described. The phenotypes **TfAA and TfBB** occur with a high frequency in all the populations investigated in the present study, while phenotypes **Tf BB** was low and phenotypes Tf AC, Tf AD, Tf BC, Tf BD and Tf CD were very low. The phenotypes **TfCC and TfDD,** however, were not obtained (Table 49).

The findings of Nishida *et al.*, (1975) on the Malaysian Katjang goats, Jamnapari and their crosses reported high frequency of Tf^B than Tf^A. Similar results were also obtained for the native goats of Thailand (Watanabe and Suzuki, 1973) and the Indonesian Etawah goats of Cerebau (Katsumata *et al.*, 1981b) and pure Katjang goats of Malaysia (Hasima, 1986). However in the present study, the frequency of Tf^A was almost high in all the populations except MARDI / IPSR and Hat Yai. The frequency ranges from 0.445 (MARDI/IPSR) to 1.00 (Hambantota and Weerawilla). Higher sample size in the present study may have caused such difference , although this observation needs to be further verified. The frequency of Tf^B of MARDI/IPSR (0.509) and Hat Yai (0.513) were slightly higher than Tf A. This agrees with the findings of Nishida *et al.*, (1975).

One possible explanation for the higher frequency of the Tf^B allele in the Malaysian goats (Nishida, *et al.*, 1975), the Philippines and Thailand native goats (Watanabe and Suzuki, 1973) and pure Katjang goat of Malaysia (Hasima, 1986) could have been due to some environmental factors in the tropical region that may have caused selection for Tf^B or non-random sampling of these animals might have led to the early establishment of Tf^B in these two countries. However, the higher frequency of Tf^A and Tf^B in the present study in most of the populations may also due to assortative mating, where mating occurs selectively between individuals having similar phenotypes, and increasing the frequency of this particular allele. On the other hand, if heterozygotes Tf AB might be having lower fitness than Tf BB then this may lead to an increase of homozygous Tf BB.

The Tf CC phenotypes have been reported only in Korea, together with Tf AC and Tf BC, by Watanabe and Suzuki (1973). They obtained Tf AC in the 'native goats of Korea, Thailand and Philippines. Similar reports on this phenotype Tf AC was observed

by Barbancho *et al.*, (1984) on two Spanish breeds, and Tf BC in a third Spanish breed, the Granadina. The incidence of Tf^C allele in various breeds of goats studied occurs in a very low frequency. These are reports from Osterhoff and Ward-Cox (1970) on the South African Angora goats (0.01); Tunon *et al.*, (1987b), on the Spanish breed, the Retinta (0.01); Nozawa *et al.*, (1987b) on the Japanese local breed of goats, the Retinta (0.01); Nozawa *et al.*, (1987b), on the Japanese local goats of Agunijima (0.01); Barbancho *et al.*, (1984) on the Spanish breeds, the Granadina (0.012), the Malaguena (0.011) and Serrana Andaluza (0.023); Watanabe and Suzuki (1973) on the Philippines native goats (0.019) and Thailand native goats (0.016), Indian goats (Bhat, 1986; Kumar and Yadav, 1988) and Hasima (1986) on the pure Malaysian Katjang goats (0.006).

In the present study the incidence of Tf^C allele was only observed in the MARDI / IPSR (0.018), Sarawak (0.014), Bogor (0.030), Ujung Pandang (0.042), Medan (0.010), Musuan (0.039) and Chengmai (0.020), goat populations. In all cases, however, Tf^C occurs in a very low frequency. The phenotype Tf AC only occurred in 2 individuals of Sarawak, one individual of Medan and 3 individuals of Musuan. Phenotype Tf BC was only observed in 2 individuals of MARDI/IPSR, 3 individuals of Bogor, 1 individual of Ujung Pandang, 1 individual of Musuan and 2 individuals of Chengmai. The Tf^D was observed in only 1 individual of MARDI/IPSR as phenotype Tf AD, 3 individuals of Ujung Pandang as phenotype Tf CD and 1 individual of Medan as phenotype Tf AD. The only other report of Tf^D, occurring with a frequency 0f 0.01, is that of Osterhoff and Ward-Cox (1970) in South African abortuses of Angora goats.

In most of the reports, frequencies of Tf^C and Tf^D had been very low, the population sample sizes did not give an unambiguous estimate of the incidence of Tf AC, Tf BC, Tf AD and Tf CD. However, differences among populations were

greater for Tf locus with Tf^A ranging from 0.445 to 1.000; Tf^B range of 0.192 to 0.309 and not present in two populations; Tf^C range of 0.010 to 0.039 and not present in six populations, and Tf^D range of 0.007 to 0.039 and not present in nine populations. The Tf^D allele is reported here for the first time in Southeast Asian goats, although at low frequency in only one population, it is quite widespread throughout the region.

The low frequency of Tf^C world wide indicates that it is a recessive marker. There is a possibility that the allele Tf^C is not highly adaptable to the environment except in Korea. In breeding programmes selection against other traits may have produced a correlated response against the**Tf CC** phenotypes. The persistence of the heterozygous Tf AC and Tf BC phenotypes in the present study and elsewhere, even showing lower frequency, may support this possibility.

The absence of allele Tf^B in the Hambantota and Weerawilla animals implies the occurrence of the founder principle (Ford, 1964). It may also suggest that the presence of other unfavorable environmental elements towards that allele. Inbreeding also increases the frequency of homozygotes. The complete level of homozygosity for Tf^A in both the populations could also be due to assortative mating, where mating occurs selectively between individuals having similar phenotype characters. Hence, assortive mating has an effect similar to that of inbreeding and increases the frequency of homozygous.

Populations from MARDI/IPSR, Sabah, Sarawak, Bogor, Medan, Musuan, Chengmai, Hat Yai, Thambuthegama and New South Wales were in Hardy-Weinberg equilibrium. Only the Ujung Pandang goat population may have the adverse effects of the factors which cause inequilibrium.

Table 48. Summary of gene frequencies of transferrin from various breeds of goats

Breeds /or Locality	(No)	Tf^A	Tf^B	Tf^C	Tf^D	Reference
Native Norwegian	(108)	No polymorphism				Efremov & Braend (1965)
Luciana (S. Italy)	(100)	0.835	0.165	-	-	Salerno *et al.*, (1968)
South Africa						
Indigenous	(57)	0.72	0.28	-	-	Osterhoff& Ward-Cox (1979)
Boer	(212)	0.70	0.30	-	-	Osterhoff& Ward-Cox (1979)
Angora (aborters)	(110)	0.76	0.23	-	0.01	Osterhoff& Ward-Cox (1979)
Angora (non-aborters)	(147)	0.80	0.19	0.01	-	Osterhoff& Ward-Cox (1979)
Bulgaria						
Toggenburg	(134)	1.00	-	-	-	Tjankov (1970)
Indigenous	(127)	0.771	0.229	-	-	Tjankov (1970)
Toggenburg	(134)	0.988	0.012	-	-	Odermatt (1973)
Bundes-Strahlen	(127)	0.960	0.040	-	-	Odermatt (1973)
Philippines						
Native goats	(80)	0.763	0.219	0.019	-	Watanabe & Suzuki (1973)
Thailand						
Native goats	(79)	0.317	0.677	0.006	-	Watanabe & Suzuki (1973)
Malaysian goats						
Peninsular Malaysia	(28)	0.430	0.570	-	-	Nishida *et al.*, (1975)
East Malaysia	(35)	0.780	0.220	-	-	Nishida *et al.*, (1975)
Jamnapari breed	(10)	0.550	0.950	-	-	Nishida *et al.*, (1975)
Japanese local goats						
Iheyajima	(41)	0.976	0.024	-	-	Nozawa *et al.*, (1978b)
Izenajima	(25)	0.980	0.020	-	-	Nozawa *et al.*, (1978b)
North Okinawa	(16)	0.993	0.067	-	-	Nozawa *et al.*, (1978b)
Agunijima	(51)	0.920	0.070	0.010	-	Nozawa *et al.*, (1978b)
Zamanijima	(25)	1.00	-	-	-	Nozawa *et al.*, (1978b)
Yonagunijima	(27)	0.982	0.018	-	-	Nozawa *et al.*, (1978b)
South Daitojima	(28)	1.00	-	-	-	Nozawa *et al.*, (1978b)
Japanese Saanen	(71)	1.00	-	-	-	Nozawa *et al.*, (1978b)

(Contd).

Table 48. Summary of gene frequencies of transferrin from various breeds of goats.

Breeds /or Locality	(No)	Tf^A	Tf^B	Tf^C	Tf^D	Reference
Indonesian Katjang goats						
Kiaralawang	(13)			-	-	Katsumata *et al.*, (1981b)
Ciangsa	(17)			-	-	Katsumata *et al.*, (1981b)
Pasar Padang	(15)			-	-	Katsumata *et al.*, (1981b)
Indonesian Etawah goats						
Cianjur	(17)	0.65	0.35	-	-	Katsumata *et al.*, (1981b)
Cerebon	(13)	0.31	0.69	-	-	Katsumata *et al.*, (1981b)
Japanese Saanen breeds						
National Institute of Animal Industry	(33)	0.788	0.212	-	-	Katsumata *et al.*, (1981b)
Angora	(21)	0.952	0.048	-	-	Katsumata *et al.*, (1981b)
Fukuoka	(46)	0.851	0.149	-	-	Katsumata *et al.*, (1981b)
Okinawa	(10)	0.913	0.087	-	-	Katsumata *et al.*, (1981b)
Korean native goats						
Kyong-sang-puk	(49)	0.959	0.041	-	-	Katsumata *et al.*, (1981b)
Cheng-do, Kyong-sang-puk	(24)	1.00	-	-	-	Katsumata *et al.*, (1981b)
Kwang-ju, Chol-la-nam	(11)	0.955	0.045	-	-	Katsumata *et al.*, (1981b)
Kwang-yong, Chol-la-nam	(35)	0.986	0.014	-	-	Katsumata *et al.*, (1981b)
Kim-hae, Kyong-sang-nam	(50)	0.980	0.020	-	-	Katsumata *et al.*, (1981b)
Pusan	(21)	0.976	0.024	-	-	Katsumata *et al.*, (1981b)
Spanish goat breeds						
Granadina	(78)	0.825	0.163	0.01	-	Barbancho *et al.*, (1984)
Muruana	(133)	0.891	0.109	-	-	Barbancho *et al.*, (1984)
Malgghena	(96)	0.703	0.286	0.011	-	Barbancho *et al.*, (1984)
Serrana Andaluza	(110)	0.932	0.045	0.023	-	Barbancho *et al.*, (1984)
Pure Katjang goat	(241)	0.335	0.659	0.006	-	Hasima (1986)

(Contd).

Table 48. Summary of gene frequencies of transferrin from various breeds of goats.

Breeds /or Locality	(No)	Tf^A	Tf^B	Tf^C	Tf^D	Reference
Spanish breeds						
Pirenaica	(115)	0.95	0.05	-	-	Tunon *et al.*, (1987b)
Verata	(100)	0.95	0.05	-	-	Tunon *et al.*, (1987b)
Guadarrama	(101)	1.00	-	-	-	Tunon *et al.*, (1987b)
Zamorana	(110)	0.99	0.01	-	-	Tunon *et al.*, (1987b)
Berciana	(100)	0.97	0.03	-	-	Tunon *et al.*, (1987b)
Granadina	(101)	0.86	0.14	-	-	Tunon *et al.*, (1987b)
Blanca Andaluza	(100)	1.00	-	-	-	Tunon *et al.*, (1987b)
Blanca Celtiberica	(110)	0.98	0.02	-	-	Tunon *et al.*, (1987b)
Murciana	(100)	0.73	0.27	-	-	Tunon *et al.*, (1987b)
Negra Serrana	(100)	0.91	0.01	-	-	Tunon *et al.*, (1987b)
Malaguena	(100)	0.80	0.20	-	-	Tunon *et al.*, (1987b)
Canaria	(99)	1.00	-	-	-	Tunon *et al.*, (1987b)
Palmera	(36)	0.74	0.20	-	-	Tunon *et al.*, (1987b)
Retinta	(108)	0.99	-	0.01	-	Tunon *et al.*, (1987b)
South African breeds						
Boer	(216)	0.58	0.42	-	-	Osterhoff *et al.*, (1987)
Native	(217)	0.79	0.21	-	-	Osterhoff *et al.*, (1987)
Saanen	(150)	0.61	0.39	-	-	Osterhoff *et al.*, (1987)
Angora	(150)	0.79	0.21	-	-	Osterhoff *et al.*, (1987)

Table 49. Gene frequencies of transferrin from the present study.

Breeds / or Locality	(No)	Tf^A	Tf^B	Tf^C	Tf^D
Malaysia					
MARDI/IPSR	(55)	0.445	0.509	0.018	0.027
Sabah	(48)	0.765	0.235	-	-
Sarawak	(71)	0.556	0.423	0.014	0.007
Indonesia					
Bogor	(50)	0.680	0.290	0.030	-
Ujung Pandang	(48)	0.604	0.323	0.042	0.031
Medan	(50)	0.750	0.230	0.010	0.010
Philippines					
Musuan	(51)	0.618	0.343	0.020	-
Thailand					
Chengmai	(50)	0.610	0.370	0.020	-
Hat yai	(39)	0.487	0.513	-	-
Sri Lanka					
Hambantota	(10)	1.00	-	-	-
Weerawilla	(37)	1.00	-	-	-
Thambuthegama	(31)	0.952	0.048	-	-
Australia					
New South Wales	(52)	0.808	0.192	-	-

5.12. X-protein

When goat cell lysates are subjected to electrophoresis and stained with a protein stain, the more anodal visible zone has been given the designation of X protein (Tucker & Clarke, 1980; Tucker *et al.*, 1983). Two phenotypes X-positive and X negative, have been described in goats by these authors and Tunon *et al.*, (1987b). Barbancho *et al.*, (1984) denoted the X negative conditions in which no protein is produced as X null (X-O). The X-positive shows a appreciable level of difference in the intensity of colouring of bands, perhaps due to hormonal and seasonal effect, as indicated for sheep (Fesus and Ramusen, 1971).

In accordance to this study, four phenotypes were observed that included two new phenotypes. The X-protein with a faster mobility than X-positive, was designated as Xp-1, the slower band (X positive) was disunited as Xp-2, the heterozygote as Xp 1-2, and the null (X-negative) condition as Xp-O. Since the effects of the Xp^{1} and Xp^{2} alleles are both expressed in the heterozygotes, they must be codominant. These phenotypes for the protein system was observed by Hasima *et al.*, (1988) and confirmed by Tucker (pers. comm., 1992) (Table 50).

The occurrence of the X-null phenotype indicates the possibility that the X-protein system may be comparable to the human ABO blood group system. In the ABO blood group system, the O allele is called the 'null allele' because no enzyme appears to be produced in the heterozygote, and therefore shows recessive gene action (Strickberger, 1985).

Similarly, in X-protein, the Xp^{O} allele may be assumed to be recessive, possibly as a consequence of a defective or absent enzyme whose phenotype effect can be masked

in the heterozygote by the functioning Xp1 and Xp2 enzymes. The Xp null (X negative) phenotype can then be redesignated as Xp O and would have the genotype Xp-O-O. The phenotype Xp1 could therefore have the genotype Xp 1-1 or Xp 1-0, and the Xp-2 phenotype could have an Xp 2-2 or Xp 2-0 genotype. Family studies conducted by Hasima *et al.*, (1988) and also the results of the present study tends to confirm that the locus is controlled by two codominant alleles.

This protein system shows considerable genetic variability in all the populations, although in 12 of the 13 populations studied there was a predominance of animals with the Xp-2 phenotype (Table 51), a situation reported by Tucker *et al.*, (1983), Barbancho *et al.*, (1984), Hasima (1988) and Tunon *et al.*, (1987). Only the New South Wales goat population produced a majority of animals with the Xp-1 phenotype. There may have been some selective advantage for this allele in New South Wales population, although why is this happening cannot be ascertained at present. There are great difference from population to population, in gene frequencies values for Xp-2, which ranged from 0.192 (New South Wales) to 0.710 (Bogor). The MARDI/IPSR, Sabah, Sarawak, Bogor, Ujung Pandang, Medan, Musuan, Hat Yai, Hambantota, Weerawilla and Thambuthegama goat samples had all the four phenotypes probably because there was no selective pressure against any of the 3 alleles. Tucker *et al.*, (1983) reported high frequencies for Xp-2 phenotype in Saanen, Toggenburg and Nubian breeds in the United Kingdom. In South African local goats, Boer, Angora, Saanen and various crossbreds, they observed similar frequencies of Xp-2 phenotype. Barbancho *et al.*, (1984) working on four Spanish breeds revealed high frequency of Xp-2 phenotype.

Except for population from MARDI/IPSR, Medan, Hambantota, Weerawilla and New South Wales, all the other eight populations were significantly deviating from Hardy-Weinberg equilibrium.

Table 50. Summary of gene frequencies of X-protein from various breeds of goats

Breeds /or Locality	(No)	Xp^1	Xp^+ (Xp 2)	Xp^- (Xp null)	Reference
British Saanen	(122)	-	0.850	0.150	Tucker *et al.*, (1983)
South African goats					
Boer	(48)	-	1.000	-	Tucker *et al.*, (1983)
Angora	(7)	-	0.570	0.430	Tucker *et al.*, (1983)
Saanen	(10)	-	1.000	-	Tucker *et al.*, (1983)
Spanish breeds					
Granadina	(80)	-	0.875	0.125	Barbancho *et al.*, (1984)
Murciana	(133)	-	0.444	0.556	Barbancho *et al.*, (1984)
Malagnina	(96)	-	0.812	0.188	Barbancho *et al.*, (1984)
Serrana Andaluza	(110)	-	0.964	0.036	Barbancho *et al.*, (1984)
Spanish breeds					
Pirenaica	(115)	-	0.640	0.360	Tunon *et al.*, (1987b)
Verata	(100)	-	0.680	0.320	Tunon *et al.*, (1987b)
Guadarrama	(101)	-	0.320	0.680	Tunon *et al.*, (1987b)
Zamorana	(110)	-	0.440	0.560	Tunon *et al.*, (1987b)
Berciana	(100)	-	0.610	0.390	Tunon *et al.*, (1987b)
Granadina	(101)	-	0.410	0.590	Tunon *et al.*, (1987b)
Blanca Andaluza	(100)	-	0.470	0.530	Tunon *et al.*, (1987b)
Blanca Celtiberica	(110)	-	0.630	0.370	Tunon *et al.*, (1987b)
Murciana	(100)	-	0.230	0.770	Tunon *et al.*, (1987b)
Negra Serrana	(100)	-	0.450	0.550	Tunon *et al.*, (1987b)
Malaguena	(100)	-	0.550	0.450	Tunon *et al.*, (1987b)
Canaria	(99)	-	0.150	0.850	Tunon *et al.*, (1987b)
Palmera	(36)	-	0.500	0.500	Tunon *et al.*, (1987b)
Retinta	(108)	-	0.710	0.290	Tunon *et al.*, (1987b)
Malaysian Katjang goats					
University of Malaya	(56)	0.002	0.124	0.354	Hasima (1986)
Kuala Selangor	(61)	0.077	0.637	0.286	Hasima (1986)
MARDI	(128)	0.008	0.737	0.225	Hasima (1986)

Table 51. Gene frequencies of X-protein from the present study

Breeds / or Locality	(No)	X^1	X^2	X^n (null)
Malaysia				
MARDI/IPSR	(55)	0.219	0.527	0.255
Sabah	(51)	0.206	0.618	0.176
Sarawak	(64)	0.344	0.563	0.094
Indonesia				
Bogor	(50)	0.200	0.710	0.090
Ujung Pandang	(48)	0.188	0.594	0.218
Medan	(51)	0.120	0.560	0.320
Philippines				
Musuan	(51)	0.196	0.618	0.180
Thailand				
Chengmai	(50)	0.200	0.470	0.330
Hat yai	(39)	0.346	0.654	-
Sri Lanka				
Hambantota	(10)	0.400	0.400	0.200
Weerawilla	(37)	0.306	0.569	0.125
Thambuthegama	(31)	0.258	0.371	0.371
Australia				
New South Wales	(52)	0.808	0.192	-

As it could be observed from each locus examined there are some populations not in Hardy-Weinberg equilibrium. This might have been caused by one or more of the following factors: assortative mating, migration, selection and genetic drift. Factors such as these and/or combination of them are most significant especially with sampling done in small-holder farms in villages. In institutional herds like the one in MARDI/IPSR and Hat Yai, the individuals that comprise them are animals that have been derived, either directly or indirectly from farms in various areas.

5.13. Monomorphic loci

In practice, the number of loci studied is often limited because of technical difficulties, and in most electrophoretic studies less than 30 loci have been examined. In this case, a large number of individuals per locus still help to reduce the standard error of average heterozygosity. This is particularly so when average heterozygosity is high. If the number of loci examined is about 25, it is recommended that at least 20-30 individuals be examined for each locus (Nei, 1987).

In the present study, the proportion of following monomorphic loci ranged between 70-77.5% and a minimum of 25 individuals was examined for each locus (Except Hambantota N = 10) for the total of forty loci.

Alkaline phosphatase, Adenylate kinase, Biliverdin reductase, 2-3 Diphosphoglyceromutase, Fructokinase, Fructose -1, 6- diphophatase, Fumarase, Glucose dehydrogenase, Esterase-2, Glucose phosphate isomerase, Glutamate oxaloacetate transaminase, Glutamate pyruvate transaminase, α-Glycerophosphate-3-phosphate dehydrogenase, Glutathione reductase, Hexokinase, Isocitrate dehydrogenase, Lactate dehydrogenase, Mannose phosphate Isomerase, NADPH-

Diaphorase 2, Peptidase-A, Peptidase-B, Peptidase-C, Peptidase-D, Phosphoglucomutase-2, Pyruvate kinase, 6-Phosphogluconate dehydrogenase, Sorbitol dehydrogenase and Superoxide dismutase showed no genetic variance between and within populations. The presence of these monomorphic loci could be due to the absence of any mutation in those loci which have kept the wild type form intact. This may also be due to:

(i) selection against recurrent mutants

and (ii) random drift, followed by the fixation of an allele and the elemination of its alternative form.

Nei and Roychoudhury (1974b), Nei (1978) and Gorman and Rezzi (1979) explained that in electrophoretic surveys a large number of loci should be examined even if the number of individuals per locus is small. The reason for this is that in almost all natural populations the variation in single-locus heterozygosity among loci is so great that average heterozygosity cannot be estimated adequately unless the number of loci studied is large. Appendix 8 shows the observed distribution of single-locus heterozygosity for three different organisms together with the theoretical distribution for neutral alleles. It is clear that in all cases the distribution is L-shaped and 60-70 percent of loci show no genetic variability (monomorphism).

5.14. Proportion of Polymorphic loci

Electrophoretically detectable genetic variability maintained in a population has been quantified in wild animal species of diverse taxonomic position. These work have shown that the proportion of polymorphic loci is in the range of 25-40% (Selander *et al.*, 1970) except in the cases of species having a small breeding size and/or an isolated

habitat (Avice and Selander 1972); Turner 1974; Nevo *et al.*, 1974; Nozawa *et al.*, 1975).

The proportion of polymorphic loci obtained from various goat populations includes the Japanese local goats for 25.9% and Japanese Saanen for 11.1 % (Nozawa *et al.*, 1987b); Japanese Saanen for 21.16 % (Katsumata *et al.*, 1981a); Korean native goats for 12.50 % (Katsumata *et al.*, 1982); Sri Lankan native goats for 6-15.9 % (Shotake *et al.*, 1986) and the Indonesian goats for range of 7.1-14.3 % (Katsumata *et al.*, 1981b). The proportion of polymorphic loci in the above mentioned studies seems to be lower because the sample size is smaller.

In the present study, the proportion of polymorphic loci show values ranging from 22.5-30.0 %. The value obtained is higher than any of the studies done earlier in the goat populations. This is due to relatively large number of individuals per locus studied as compared to the earlier studies on goats.

5.15. Heterozygosity (Gene diversity)

A more appropriate and one of the most important measures of genetic variability of populations is to obtain an estimate of **heterozygosity** or **gene diversity**. This measure does not depend on the arbitrariness of the definition of polymorphism, it can be defined unambigously in terms of gene frequencies.

The extent of protein polymorphism is measured by average heterozygosity. Average heterozygosity varies from organism to organism. Nei and Gaur (1984) reported that vertebrates tend to show a lower heterozygosity than invertebrates. In most of their studies on various species in which there are 20 or more loci, the average heterozygosity is generally lower than 0.1 in vertebrates and rarely exceeds 0.15, but

there are many species showing a value between 0.1 and 0.4. (Appendix 9). The highest level of gene diversity so far observed is that of bacteria (H=0.48 based on 20 loci in *Escherichia coli*, Selander and Levin, 1980; In vertebrates H=0.49 based on 29 loci was observed in *Klebsiella oxytoca* (Howard *et al*,., 1985).

The average heterozygosity in wild animals has been quantified to be in the range of 0.05 to 0.15 (Selander *et al.*, 1970) except in the cases of species having a small breeding size/or an isolated habitat (Avise and Selander, 1972; Turner, 1974; Nevo *et al.*, 1974; Nozawa *et al.*, 1975). In domestic animals, on the other hand, Nozawa *et al.*, (1976) made a comparative electrophoretic analysis on the Asian and European horse breeds and showed that the genetic variability were about the same level as the wild animal populations.

The average heterozygosity of the various goat population studied so far are the Japanese Saanen goats, 0.0483 (Katsumata *et al.*, 1981a), Sri Lankan native goats with a range of 0.0199 to 0.0469 (Shotake et al., 1986, Korean native goats, 0.0250 (Katsumata *et al.*, 1982), and Indonesian goats with a range of 0.0312 to 0.0513 (Katsumata *et al.*, 1981b). In the present study the average heterozygosity obtained ranged from 0.118 (Thambuthegama) to 0.311 (Hambantota). From these values it can be considered that the genetic variabilities for all these locations are very low. However, the genetic variability from the present study and also from studies conducted on various goat populations revealed that there is markedly lower variability than in most wild species and domestic horses. This observation is in contrast to the earlier report of Nozawa *et al.*, (1976).

From the results, it is important to note that the observed heterozygosity in the goat populations is generally lower than the expected heterozygosity. Nei and Gaur (1984) and Nei *et al.*, (1975c) interpreted this phenomena as being due to the reduction in

population size (bottleneck effect) that could have occurred (Appendix 10). On the other hand, there are other possibilities that reduce the level of genetic variability in these populations i.e. inbreeding in some populations and high selection against male breeders in other populations

The generally observed deficiency of heterozygotes may be indicative of genetic drift in population of small effective size and the occurrence of deliberate inbreeding. The type of selection prevailing must have increased the inbreeding coefficient which may lead to the lower fitness of heterozygotes. Both Weerawilla (0.034) and Thambuthegama (0.029) showed lower level of mean heterozygosity than the other populations. Isolated populations usually show a lower heterozygosity than large populations (Selander *et al.*, 1971; Nei, 1983 and Nei and Gaur, 1984).

It may have also resulted from the Wahlund effect, animals under investigation may include several mating units and sub-populations, hence, the frequency of homozygotes tends to be higher than the Hardy-Weinberg proportion. The contingency chi-squares of the polymorphic loci show that this, in fact, is true for the population from which the goats have been sampled.

Many workers have also examined the relationship between heterozygosity and environmental factors such as temperature, humidity, availability of resource, in the hope of identifying the environmental determinants of genetic variability (Bryant, 1974; Powel, 1975; Valentine, 1976; Nevo *et al.*, 1984). However, critical reviews of these works have shown that many of the correlations identified are just spurious and do not indicate real causal relationships (Schnell and Selander, 1981; Nei and Gaur, 1984).

Quaternary structure of protein plays an important role in determining the heterozygosity level (Zourous, 1976; Harris et al., 1977; Ward, 1977 and Koehn & Eanes, 1978). They noticed that in several species of animals and plants monomeric

enzymes consisting one of polypeptides tend to show a higher heterozygosity than multimeric enzymes. Similar observations were also observed in the present study as illustrated in Table 52. The proportion of polymorphic (P) loci is higher for monomers than for dimers, which in turn showed higher values of P than tetramers. In the case of trimers, only one polymorphic locus was identified in the only one examined. The reason for multimeric enzymes showing a lower degree of polymorphism due to the higher degree of functional constraint because different polypeptides have to form a single functional protein (Koehn and Earnes, 1978; Kimura, 1983).

5.16. Deviation from Hardy-Weinberg Proportion

Hardy-Weinberg equilibrium holds for many polymorphic loci in outbreeding organisms. However, it can be disturbed by a number of factors such as inbreeding, assortative mating and natural selection. Inbreeding increases the frequency of homozygotes, and if there is no other factor, F is equal to Wright's (1969) inbreeding coefficient. Selection may increase or decrease the F value, depending on the type of selection. Deviations from Hardy-Weinberg equilibrium occur solely by inbreeding or random differentiation of gene frequencies among subpopulations.

Wahlund (9182) showed that the gene frequency differences among subdivided populations cause a deficiency of heterozygotes compared with the case of single random mating population. Wright (1943, 1965, 1969) proposed to measure the deviation of genotype frequencies in a subdivided population in terms of three parameters, F_{IS}, F_{IT} and F_{ST}, which is called **fixation indices** or **F-statistics**. Nei and Chesser (1983) and Weir and Cockerham (1984) defined fixation indices in terms of population gene and genotype frequencies.

Table 52. Proportion of polymorphic loci (P) for monomeric, dimeric, trimeric and tetrameric enzymes in the present study of goat populations.

Subunit Structure	**Number of loci**	**(P)**
Monomeric	18	0.444
Dimeric	14	0.143
Trimeric	1	1.000
Tetrameric	7	0.142
Total	***40***	***0.300***

The F-statistics in the present study shows substantial amount of inbreeding within population (F_{IS}) for Ca, Me, Mdh, Dia-1, Dia-2 and Xp loci. This suggests the possibility that either selection or non-random mating or both caused an excess of homozygotes in these loci. F_{IT} is quite large (0.499), and this is largely due to F_{IS} (= 0.277) rather than to F_{ST} (= 0.163). The fixation indices for individual loci, particularly F_{IS} and F_{IT}, vary considerably. The estimate of F_{ST} is 0.163, which is significantly different from O (zero). Such a marked differentiation is considered to be caused by random genetic drift due to small effective size of each population and by bottleneck effect which could be occurring at the time of introduction of breeding individuals, mainly breeding males, into each populations.

5.17. **Genetic Distance**

There are many geneticists who were interested in the study of the extent of genetic differences between populations or species, and therefore various measures of genetic distance were proposed [Czekanowski, 1909; Pearson (1926); Fisher (1936); Mahalanobis (1936); Cavalli-sforza and Edwards (1964, 1975), Wright (1951), Nei (1971, 1972) and Rogers (1972)].

The standard genetic distance method of Nei (1972) has been used extensively in studies of evolutionary genetics of natural populations and in some livestock studies. The basic principle of this method is that any allelic differences in electrophoretic mobility is caused by at least one codon difference at the gene level and thus the average number of codon differences per locus can be estimated from allele frequency data statistically. Since this number is a direct measure of gene differences, this is a good measure of genetic distance between populations (Nei, 1987). This distance measure

also seems to be superior to other distance measures, since it is less sensitive to sampling error (Nei, 1987).

Among the studies carried out in livestock are the genetic distance among seven Spanish native cattle breeds, which ranged from 0.007 to 0.180 (Gonzalez *et al.*, 1987), the genetic distances among four pig breeds of Europe, ranging from 0.0693-0.1030 (Van Zeveren *et al.*, (1990) and the genetic distance among five Italian native sheep breeds ranging from 0.0124-0.0599 (Zanotti Casati *et al.*, 1990).

For goats, few studies of genetics distances have been undertaken for various breeds. The genetic distance among eight Okinawa populations in Japan ranged from 0.0004-0.0025 (Nozawa *et al.*, 1987b). the genetic distance among seven native population of Indonesia ranged from 0.0011 to 0.0174 (Katsumata *et al.*, 1981b), the genetic distance among seven population of Japanese Saanen ranged from 0.004-0.0065 (Katsumata *et al.*, 1981a), the genetic distance of six native goat populations of Korea ranged from 0.0001 to 0.0056 (Katsumata *et al.*, 1982) and finally the genetic distance of fourteen native Spanish breeds ranged 0.003 to 0.097 (Tunon *et al.*, 1989). These distances among Spanish breeds, which are substantially larger than the distance among local populations of native goats within countries in Asia, were based on relatively larger samples from each breed (36-115) and eight polymorphic loci.

In accordance to this study, the genetic distance in the thirteen goat populations ranged from 0.001 to 0.043. However, it could be pointed out that there are still substantial genetic differences present.

Pairwase genetic distance among populations were computed using Nei's standard genetic distance, and a dendrogram produced for the populations. The dendrogram show that populations within countries do not necessarily cluster close to each other,

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Pairwase genetic distance among populations were computed using Nei's standard genetic distance, and a dendrogram produced for the populations. The dendrogram show that populations within countries do not necessarily cluster close to each other,

and there are many cases where genetic distance are not closely related to geographic distance.

The goat populations of Bogor and Ujung Pandang (Indonesia) and Hambantota and Weerawilla (Sri Lanka) have clustered together. On the other hand, Medan (Indonesia) clusters with Sabah (Malaysia), and with Chengmai (Thailand), but they are all geographically very distant. Similar results were also obtained by Nozawa *et al.*, (1987b) whose report shows that the genetic differentiation among the island population of the Okinawa goats has no relation to the geographic distance between the islands.

The Thambuthegama (Sri Lanka) and New South Wales (Australia) animals, particularly the former, differ from the rest of the goat population of Southeast Asia and Sri Lanka perhaps due to the genetic drift and high level of inbreeding or simply because of chance. The Wahlund effect might have also contributed towards the augmentation of the occurrence too.

However it must be noted that the goat populations were classified into one big cluster of nine populations and two other clusters, each involving two populations. It seems that all the nine goat populations of the big cluster belongs to Southeast Asia region. The Sri Lankan goats, like Indian breeds of goats, presumably have differentiated genetically from the rest of Southeast Asian goats. Why their relationship with Australian Feral goats, a heterogeneous mixture of European breed of goats should be much closure than their relationship with Southeast Asian goats could not be explained at this stage. A separate study needs to be done to look at the migration patterns and evaluation of goats in Sri Lanka and Australia before establishing anything towards this effect.

Chakraborty and Nei (1977) have shown that the distance increases rapidly in the presence of bottlenecks and that the rate of increase is higher when the bottleneck size is

small than when this is large. However, if the population size returns to the original level, the bottleneck effect gradually disappears (Appendix 10). Whether there are presence of such bottleneck effects in Sri Lankan and Australian goat populations need to be studied.

The genetic relationships among populations as illustrated by this dendrogram and by F-statistics indicates that the native goat populations are genetically different strains which are likely to differ also in quantitative traits important to production, such as growth.

5.18. General Discussion

It should be borne in mind that there is no general agreement on criteria concerning the origin of the domestic goat, working from conclusive data offered by various authors (Devendra and Burns, 1983; Devendra and Nozawa, 1976; Bokonyi, 1974). They considered ***Capra aegagrus*** alone may be considered as the wild ancestor of domestic goats. However, it must be realized that the dendrogram thus obtained do not offer any information concerning time, or data on the common ancestor. At this point, Nei (1975) emphasizes that the dendogram only represents genetic relationships between populations breeds, but may or may not show true evolutionary history of populations, especially when these populations are not completely isolated. Therefore, the great subdivision observed on the dendogram should not be interpreted as two independent evolutionary branches, but rather as two groups that have become genetically differentiated from ***Capra aegagrus (C. hircus)***, dueto factors like inbreeding, genetic drift of differential selection, bottle-neck effect, Wahlund effect, habitat, means of exploitation and production capacity.

It should be pointed out here that the present study is a major part of the project which investigates the genetic difference among the goat populations of Southeast Asia, Sri Lanka and Australia, and there are plans to increase the number of loci to be studied and also samples from other countries in Asia. Therefore, the genetic relationships among population as indicated by the present dendrogram and by the F statistics may well change but the qualitative conclusion are unlikely to be dramatically different. This study involving various enzyme/loci is expected to be followed by similar population study in future involving DNA loci. Representative population from each of the 3 sets may then be involved in such study which could be cost and time saving.

As the traditional husbandry system of the small farmers' units produce the bulk of livestock products, and as these systems are unlikely to change rapidly the breeding programmes for genetic improvement of currently used breeds are unlikely to be developed rapidly. Most immediate benefits will come from the use of the best population / strain. Evaluation of comparative productivity thus is vital so that the best breeds and strains for each climate-husbandry-management system can be identified and brought into wider use in that system. Steps could also now be undertaken to eliminate the potential of losing useful genetic material through indiscriminate crossing of breeds with exotic ones in determining the sets of population which are genetically more identical.

It is also important to note here that through cooperation with the animal scientists and Department of Veterinary Services in the Southeast Asia region, the research will stimulate interest in studies on the productivity of the various breeds and strains, and the comparative evaluation of selected populations. The success of this research is assured and all the countries whose goat population included in the study will benefit, provided

the appropriate evaluation studies on the selected animals are then done. The benefits here are in terms of most efficient use of limited resources and scientific manpower.