

Population Genetic Studies of the Philippine Negritos. I. A Pilot Survey of Red Cell Enzyme and Serum Protein Groups

KEIICHI OMOTO,¹ SHOGO MISAWA,² SHOJI HARADA,² JOAQUIN S. SUMPAICO,³
PACIFICO M. MEDADO,³ AND HIROSHI OGONUKI⁴

INTRODUCTION

The Negritos (also known as Aetas) are short statured, dark, frizzly-haired people who inhabit remote areas of the Philippines (fig. 1). According to a recent estimate [1], they comprise a total population of approximately 22,500. The Negritos, together with other short statured hunter-gatherers (e.g., the Semang of Malaysia and the Andamanese) are thought to be the oldest living aborigines of Southeast Asia and the western Pacific.

Recent studies based on blood group data have failed to clarify the long-standing anthropological controversy regarding the supposed relationship among the African, Asian, and Oceanic Pygmies or Negritos [2]. While little is known about the distribution of genetic markers other than the ABO blood groups [3, 4] of the Negritos, Pascasio et al. recently reported the presence of the "African genes" *V* and *J_s^a* and some probable new variants of serum proteins in a small Negrito sample (no. = 46) from Zambales, central Luzon [5].

In this paper, we report the results of electrophoretic surveys of 15 red cell enzyme and five serum protein systems from Negrito blood samples collected in the Philippines over the past 2 years. The ecological and demographic status of the Negritos will be the subject of a future study.

MATERIALS AND METHODS

Blood samples were collected by venipuncture in ACD solution from 129 healthy, unrelated Negritos from the Angeles city area, Pampanga, central Luzon, and were transported by air to Tokyo within a few days. While most individuals considered themselves pure Negrito, the degree of admixture with the non-Negrito Filipinos was not known. Among the 50 adults (aged 25 or older), there were 22 males (height: 142–160 cm; mean: 150.73 ± 6.51 cm) and 28 females (height: 127–154 cm; mean: 142.36 ± 8.91 cm).

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¹ Department of Anthropology, Faculty of Science, University of Tokyo, Tokyo, Japan.

² Department of Community Medicine, University of Tsukuba School of Medicine, Tsukuba, Japan.

³ Bureau of Research and Laboratories, Department of Health, Manila, Philippines.

⁴ Japan International Cooperation Agency, Manila, Philippines.

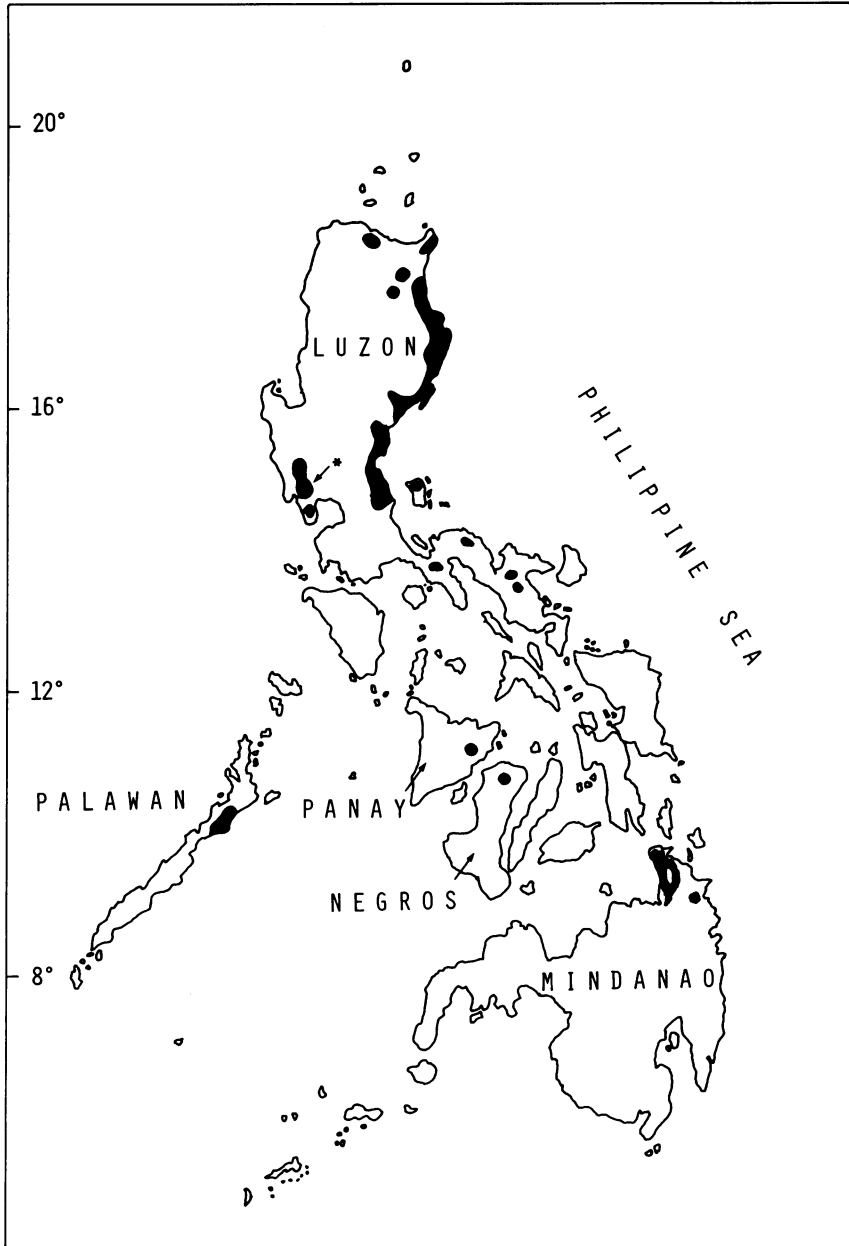


Fig. 1.—The distribution of the Negrito groups in the Philippines. Map of the Filipino people published by the National Museum of the Philippines, Manila, 1974. Blood collection center of the present study in west central Luzon is indicated by an asterisk.

After plasma was separated, hemolysates were prepared from washed, packed red cells by freezing and thawing. Examinations were made on the following red cell enzymes: acid phosphatase-1 (ACP₁), phosphoglucomutase-1 and -2 (PGM₁ and PGM₂), phosphogluconate dehydrogenase (PGD), adenylate kinase (AK), adenosine deaminase (ADA), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), phosphohexose isomerase (PHI), phosphoglycerate kinase (PGK), glutamic-pyruvic transaminase (GPT), glutamic-oxaloacetic transaminase (GOT), uridine monophosphate kinase (UMPCK), glyoxalase I (GLO), and esterase D (ESD); and the following five serum proteins: haptoglobin (Hp), transferrin (Tf), group-specific component (Gc), third complement component (C3), and alpha₁-antitrypsin (Pi). Electrophoretic conditions and staining procedures for all systems were carried out according to standard techniques [6, 7]. Horizontal starch gel electrophoresis was used with 12% starch (Connaught Laboratory, Willowdale, Ontario) for typing all systems except Gc, which was screened by conventional immunoelectrophoresis. Comparisons between Gc variants discovered in the present study and controls were made by agarose gel immunofixation electrophoresis [8]. A monospecific anti-Gc (goat) serum was obtained from Atlantic Antibodies (Westbrook, Maine).

RESULTS

Red Cell Enzymes

Among 15 red cell enzymes examined, polymorphic variation was found in nine systems (table 1); no variant was discovered in PGM₂, PHI, PGK, LDH, MDH, or GOT. Variants were unexpectedly discovered in AK and ESD. An unusual finding for this Asian-Pacific population was the occurrence of the AK 2-1 phenotype in 18 of 129 samples with an apparent *AK*² allele frequency of .07.

In esterase D, a new variant allele, denoted *ESD*^{3Negr1to}(*ESD*^{3N}), was found in a polymorphic frequency. In addition to the three common phenotypes (ESD 1, ESD 2-1, and ESD 2), three other phenotypes were found which had a variant ESD isozyme that migrated more slowly than ESD 1 (fig. 2). Two of the three variant phenotypes demonstrated a three banded pattern with a strongly stained hybrid band midway between the variant isozyme and ESD 1 and 2; these heterozygous phenotypes, denoted ESD 3N-1 and ESD 3N-2, were the only ones in the entire sample. The best results for esterase D typing were obtained using Karp and Sutton's ACP buffer, pH 5.9 [9]. Examination of relatives of ESD 3N heterozygotes revealed individuals typed as ESD 3N homozygotes with a single major ESD isozyme corresponding to the slowest band in the heterozygotes.

The six phenotypes determined by three alleles are shown in figure 2. The gene frequency of this "rare" ESD variant was estimated to be as high as $.10 \pm .019$, making it perhaps the first example of a "rare" ESD variant that occurs in polymorphic frequency.

Serum Proteins

The results of the typings of five serum proteins are presented in table 1; only alpha₁-antitrypsin showed no variation.* Conventional immunoelectrophoresis of the Gc system revealed three variant Gc phenotypes (in addition to the common types—Gc

* In the present study, only starch gel electrophoresis was used to screen Pi variants. The results, therefore, are tentative.

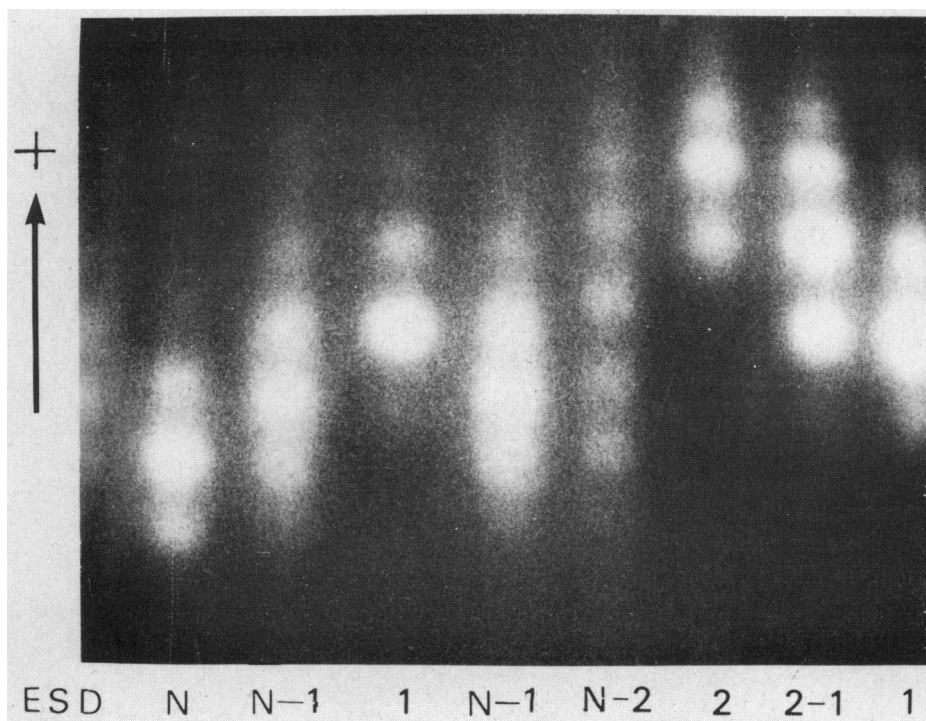


FIG. 2.—Photograph of a starch gel showing six phenotypes of esterase D found in the Negrito sample. The symbol N refers to the variant ESD isozyme determined by a possibly new allele $ESD^{3Negrito}$

1-1, Gc 2-1, and Gc 2-2) which have a Gc component that migrates faster than Gc 1. Originally we thought this variant represented the first example of Gc Ab (Gc Y) in populations outside New Guinea, Australia, and Africa, but comparisons with control samples* of Gc 1-Ab and Gc 2-Ab, using agarose gel immunofixation electrophoresis, showed this variant to be unique. As shown in figure 3a, this fast-migrating, double-banded variant is not only migrating faster than Gc Ab, but the staining intensity of two bands is the same, whereas in Gc Ab, the anodal band is stained much more strongly. Moreover, figure 3b confirms that this variant has a greater anodal mobility than Gc Japanese (Gc J). Although no comparisons were made with Gc Darmstadt, it is likely that this variant we call Gc Negrito (Gc N) is a new Gc variant. All of the three possible combinations, namely, Gc N-N, Gc 1-N, and Gc 2-N, were found. The estimated frequency for Gc^N was remarkably high: $.21 \pm .025$. Observed numbers agreed with Hardy-Weinberg equilibrium expectations.

The estimated gene frequencies for 21 loci are presented in table 2. For comparison, data from three non-Negrito Filipino populations—the Tagalog (Manila), Visayan (Negros Island), and Ifugao (Mountain province)—are given [10].

* The control samples of the Gc variants of the Australian aborigines were kindly provided by Mr. K. Kenrick, Sydney.

TABLE 1
RED CELL ENZYME AND SERUM PROTEIN PHENOTYPES IN 129 NEGRITO SAMPLES

System and Phenotype	No. Observed	%	No. Expected	χ^2
ACP_i:				
A	5	3.91	2.67	2.77
AB	27	21.09	31.65	
B	96	75.00	93.68	
Total	128	100.00	128.00	
PGM_i:				
1	32	24.81	32.25	0.04
2-1	65	50.39	64.00	
2	31	24.03	31.75	
6-2	1	0.77	0.50	
Total	129	100.00	128.50	
PGD:				
A	122	95.31	122.08	0.07
AC	6	4.69	5.85	
C	0	0.00	0.07	
Total	128	100.00	128.00	
AK:				
1	111	86.05	111.62	0.73
2-1	18	13.95	16.75	
2	0	0.00	0.63	
Total	129	100.00	129.00	
ADA:				
1	103	79.84	103.40	0.15
2-1	25	19.38	24.18	
2	1	.78	1.41	
Total	129	100.00	128.99	
GPT:				
1	2	1.55	2.65	0.22
2-1	33	25.58	31.69	
2	94	72.87	94.66	
Total	129	100.00	129.00	
GLO:				
1	8	6.20	7.69	0.02
2-1	47	36.43	47.62	
2	74	57.37	73.69	
Total	129	100.00	129.00	
UMPK:				
1	61	47.29	55.34	4.85*
2-1	47	36.43	58.30	
2	21	16.28	15.35	
Total	129	100.00	128.99	

TABLE 1 (continued)

System and Phenotype	No. Observed	%	No. Expected	χ^2
ESD:				
1	76	58.91	78.30	2.51
2-1	25	19.38	24.14	
2	2	1.55	1.86	
3N-1	24	18.60	20.26	
3N-2	2	1.55	3.12	
3N	0	0.00	1.31	
Total	129	100.00	128.99	
Hp:				
1	5	3.91	5.80	0.18
2-1	43	33.59	41.39	
2	73	57.03	73.80	
0	7	5.47	...	
Total	128	100.00	121.00	
Tf:				
C	127	99.22	127.00	0.99
CD	1	0.78	0.99	
Total	128	100.00	127.99	
Gc:				
1-1	52	41.27	49.53	5.03
2-1	21	16.67	26.34	
2-2	7	5.56	3.50	
1-N	33	26.19	32.60	
2-N	7	5.56	8.67	
N-N	6	4.76	5.36	
Total	126	100.01	126.00	
C3:				
S	103	97.17	103.01	0.003
SF	3	2.83	2.97	
Total	106	100.00	105.98	

NOTE. — The total number observed was fewer than 129 in several systems because samples were used up.

* Significant deviation from Hardy-Weinberg equilibrium ($.01 < P < .05$).

DISCUSSION

The results of electrophoretic surveys presented above show a unique distribution of phenotypes in several polymorphic systems. Some of the findings seem to be genetically and anthropologically significant.

The most striking finding was the high frequency of a "rare" esterase D allele, ESD^{3N} . Recently, Blake detected only a single example of a slow electrophoretic variant of ESD in 9,000 specimens from the Asian-Pacific [11], and only two rare, slow variant alleles (ESD^3 and ESD^4) have been reported in European populations [12–14]. Although no comparisons were made between these variants and ESD^{3N} , we

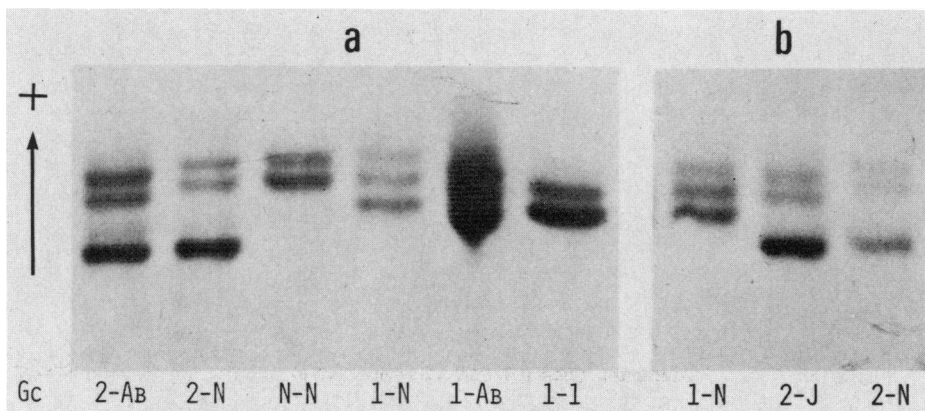


Fig. 3.—Patterns of Gc variants demonstrated by immunofixation electrophoresis, *a*, The Negrito variants compared with Gc Ab controls; *b*, comparison of Gc 1-N and Gc 2-N with Gc 2-J.

feel that the Negrito variant, while similar to *ESD*³ in electrophoretic mobility, is a distinct variant. In view of the geographically isolated occurrence, it is most likely that this variant allele arose by mutation and attained its present high frequency by random genetic drift. We also noted that this variant is common in another Negrito group living in Bataan Peninsula but is not present in the Negritos (Mamanwa) of northern Mindanao (unpublished data). To date, it has not been detected in non-Negrito Filipinos.

The second important discovery was the high frequency of the new Gc variant. To date, the most common variant of Gc is Gc Ab (Gc Y) which is found in Australia,

TABLE 2

GENE FREQUENCIES OF RED CELL ENZYME AND SERUM PROTEIN SYSTEMS OF THE NEGRITOS COMPARED WITH THOSE OF NON-NEGRITO FILIPINOS

Locus and Allele	Negrito (No. = 129)	Tagalog (No. = 253)	Visayan (No. = 125)	Ifugao (No. = 97)
<i>ACP</i> ₁ :				
A1445	.2800	.2320	.1598
B8555	.7200	.7680	.8402
<i>PGM</i> ₁ :				
15000	.7225	.7391	.8454
24961	.2700	.2565	.1495
60039	.00250051
70050	.0043	...
<i>PGM</i> ₂ :				
1	1.0000	1.0000	1.0000	1.0000
<i>PGD</i> :				
A9766	.9121	.9708	.9433
C0234	.0879	.0291	.0567
<i>AK</i> :				
19302	.9960	1.0000	1.0000
20698	.0040

TABLE 2 (continued)

Locus and Allele	Negrito (No. = 129)	Tagalog (No. = 253)	Visayan (No. = 125)	Ifugao (No. = 97)
<i>ADA</i> :				
1	.8953	.9200	.9616	.8925
2	.1047	.0800	.0304	.1075
3*0080	...
<i>LDH_A</i> :				
1	1.0000	.9960	1.0000	1.0000
Cal-I	...	0040
<i>LDH_B</i> :				
1	1.0000	1.0000	1.0000	1.0000
<i>MDH</i> :				
1	1.0000	1.0000	1.0000	1.0000
<i>PHI</i> :				
1	1.0000	.9980	1.0000	1.0000
40020
<i>PGK</i>				
1	1.0000	1.0000	1.0000	1.0000
<i>GPT_S</i>				
1	.1434	.3241	.3400	.4895
2	.8566	.6709	.6320	.4789
3*0200	...
60050	.0080	.0316
<i>GOT_S</i>				
1	1.0000	.9875	.9958	1.0000
20125	.0042	...
<i>UMPK</i>				
1	.6550	n.t.	n.t.	n.t.
2	.3450			
<i>GLO</i> :				
1	.2442	n.t.	n.t.	n.t.
2	.7558			
<i>ESD</i>				
1	.7791	.6919	.7160	.5722
2	.1201	.3081	.2840	.4278
3N	.1008
<i>Hp</i> :				
1	.2190	.3426	.3484	.3934
2	.7810	.6574	.6516	.6066
<i>Tf</i> :				
C	.9961	.9877	.9715	1.0000
D	.0039	.0123	.0285	...
<i>Gc</i> :				
1	.6270			
2	.1667	n.t.	n.t.	n.t.
N	.2063			
<i>C3</i> :				
S	.9858	n.t.	n.t.	n.t.
F	.0142			
<i>Pi</i> :				
M	1.0000	n.t.	n.t.	n.t.

NOTE. — Symbols for alleles are simplified. n.t. = not tested.

* Tentative typing.

New Guinea, and other parts of Melanesia, and Africa [15, 16]. According to Howells [17], the Negritos are ancestors of the late Pleistocene populations inhabiting "Old Melanesia," which extended from Southeast Asia, including what is now Malaysia, Indonesia, and the Philippines to the Sahulland (the land mass covering New Guinea and Australia). Therefore, if a Gc variant is present in the Negritos, one would expect that it would be Gc Ab. The present results, however, indicate that this is not the case. A detailed report of this Gc variant will be published elsewhere.

The third important finding was the occurrence of individuals with an AK variant phenotype electrophoretically indistinguishable from AK 2-1. Because AK^2 is regarded as a Caucasoid marker and because of its virtual absence in Mongoloids and Pacific Islanders [18], its frequency ($.07 \pm .016$) in Negritos was unexpected. The possibility that it has been introduced by admixture with Europeans or Indians may be excluded, based on anthroposcopic characters of the Negrito individuals with an AK 2-1 phenotype. We feel that either the AK polymorphism is a basic character of the Negrito population or that this rare variant accumulated by chance in the Negritos we examined.

It is interesting to note that an AK 2-1 individual was also found among 256 Tagalogs (Manila). Lie-Injo found AK^2 in polymorphic frequencies in the Senoi (.012) and the Malay (.015) in Selangor, but did not report any AK data for the Semang, the Negritos of Malaysia [19]. It now appears that at least some aboriginal populations of Southeast Asia and the western Pacific possess an AK variant in polymorphic frequency. It is important to determine whether the AK variant found in Asian populations is identical to AK^2 found among Europeans.

The distribution of several polymorphic genes is different in the Negritos and non-Negrito Filipinos (see table 2); for example, the Negritos are characterized by the low frequency of ACP_1^A , GPT_s^1 , ESD^2 , and Hp^1 , and an exceptionally high frequency of PGM_1^2 . While Blake reported [11] a frequency of GPT_s^1 ranging from 28% to 100% in the Asian-Pacific area, we found among the Negritos the lowest frequency of this allele ever reported. Thus, the known frequency for GPT_s^1 increases gradually as one goes north from the Philippines to central Japan. This clinal distribution in eastern Asia suggests that the low GPT_s^1 frequency of the Negrito sample may not be accidental but may be reminiscent of the genetic characteristics of the aboriginal populations of Southeast Asia or the western Pacific.

While the two common alleles, PGM_1^1 and PGM_1^2 , were found in the same frequency (.50) in our sample, the frequency of PGM_1^2 in Oceania ranges from .01 to .16 and in east Asia, from .17 to .27 [20]. The frequency is somewhat higher in India (.26-.34) with the exception of two aboriginal minority groups, namely, the Kadar of Kerala (.43, no. = 213) and the Irulas, Todas, and Kurumbas (.45, no. = 316) of the Nilghiri Hills. (The latter figure is the most similar to the present Negrito sample.)

Although it may be coincidental, it is interesting to note that the Kadars have Negrito-like features and are considered by some anthropologists to be a true Negrito group [21]. A unique variant allele detected in Kadar, PGM_1^{6Kadar} , however, was not found in our sample.

In all the polymorphic systems examined, observed phenotypic frequencies are in good agreement with the expected except for UMPK, in which a heterozygote deficit

was observed ($\chi^2 = 4.85$, 1 df, $.01 < P < .02$). This result, however, needs confirmation.

The heterozygosities calculated for 21 loci are presented in table 3. The corresponding values in Japanese—a large, relatively homogeneous population—were contrasted with the Negritos. While the proportion of polymorphic loci was essentially the same for two populations (i.e., 12 in 21 in Negritos and 13 in 21 in Japanese), the average heterozygosity of the Negrito sample (.1649) is slightly higher than the Japanese (.1401), the latter based on a larger sample size [22–27]. The high heterozygosity of our small sample, together with the occurrence of unique alleles at polymorphic frequencies, was rather surprising given the small, isolated nature of the Negritos. Although gene flow from surrounding non-Negrito populations may have played a role, it seems likely that subdivision of the Negrito population into small, semi-isolated breeding units and occasional gene exchange among these maintained a high degree of allelic variability.

TABLE 3
COMPARISON OF THE AVERAGE HETEROZYGOSITY FOR 21 LOCI BETWEEN THE NEGRITO AND JAPANESE POPULATIONS

System	NEGRITO		JAPANESE*	
	No. Polymorphic Alleles	Heterozygosity	No. Polymorphic Alleles	Heterozygosity
Red Cell Enzymes:				
PGM ₁	2	.5039	2	.3906
UMPK	2	.4520	2	.1000
GLO-1	2	.3691	2	.1610
ESD	3	.3684	2	.4503
ACP ₁	2	.2472	2	.3509
GPT _S	2	.2457	2	.4739
ADA	2	.1875	2	.0411
AK	2	.1299	1	.0000
PGD	2	.0457	2	.1421
GOT _S	1	.0000	2	.0225
PGM ₂	1	.0000	1	.0000
PHI	1	.0000	1	.0000
PGK	1	.0000	1	.0000
LDH _A	1	.0000	1	.0000
LDH _B	1	.0000	1	.0000
MDH	1	.0000	1	.0000
Average15931333
Serum Proteins:				
Gc	3	.5365	2	.3509
Hp	2	.3420	2	.3848
C3	2	.0280	2	.0257
Tf	1	.0078	1	.0198
Pi	1	.0000	2	.0276
Average18291618
Combined Total16491401

* Calculated by taking the average of a number of published data [22–27].

The present study and that of Pascasio et al. [5] are the first attempts to elucidate the genetic structure of the Philippine Negrito population. More data from Negrito groups in other parts of the Philippines are needed to identify factors maintaining allelic diversity, as well as the genetic origins of the Negritos.

SUMMARY

Electrophoretic surveys of red cell enzyme and serum protein systems representing 21 genetic loci were carried out on 129 blood samples of the Negritos of Pampanga, Central Luzon, the Philippines. Nine (out of 16) red cell enzyme loci and four (out of five) serum protein loci showed polymorphic variation. Low frequencies of ACP_1^A , GPT_S^1 , ESD^2 , and Hp^1 , and a markedly high frequency of PGM_1^2 were contrasted to those in non-Negrito Filipinos. Variant ESD phenotypes with a slowly migrating isozyme occurred in high frequency. The new allele designated as $ESD^{3Negrito}$ (ESD^{3N}) had a frequency of $.10 \pm .019$. In AK, a variant phenotype indistinguishable from AK 2-1 was observed in 14% of the sample. In the Gc system, a fast migrating variant was discovered in high frequency which was distinct from Gc Ab and Gc J. The variant allele, denoted $Gc^{Negrito}$ (Gc^N), had a frequency of $.21 \pm .025$. A relatively high degree of allelic diversity in the Negrito sample was also suggested by the average heterozygosity for 21 loci screened (.165), which is compared to that of the Japanese population (.140).

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