Anthropological Implications of Sickle Cell Gene Distribution in West Africa[1]

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DURING the past fifteen years, data on the frequency of the sickle cell gene have accumulated to such an extent that its world distribution can now be outlined in considerable detail. Frequencies of more than 20 percent of the sickle cell trait have been found in populations across a broad belt of tropical Africa from the Gambia to Mozambique. Similar high frequencies have been found in Greece, South Turkey, and India. At first it appeared that there were isolated "pockets" of high frequencies in India and Greece, but more recently the sickle cell gene has been found to be widely distributed in both countries (Choremis and Zannos 1956; Sukumaran, Sanghvi, and Vyas 1956). Moreover, between these countries where high frequencies are found, there are intermediate frequencies, in Sicily, Algeria, Tunisia, Yemen, Palestine, and Kuwait. Thus, the sickle cell gene is found in a large and rather continuous region of the Old World and in populations which have recently emigrated from this region, while it is almost completely absent from an even larger region of the Old World which stretches from Northern Europe to Australia.

When the broad outlines of the distribution of the sickle cell gene first began to emerge, several investigators attempted to explain various aspects of this distribution by migration and mixture. Lehmann and Raper (1949) attempted to show that the differences in the frequency of the sickle cell gene among the Bantu tribes of Uganda were due to varying degrees of Hamitic admixture; Brain (1953) and Lehmann (1954) postulated migrations from Asia to account for the distribution of the sickle cell gene in Africa; and Singer (1953), using an age-area type of argument, postulated that the sickle cell gene arose by mutation near Mt. Ruwenzori and diffused from there. However, it was recognized early in the development of the sickle cell problem that regardless of the extent to which migration and mixture explained the distribution pattern of the sickle cell gene, its high frequencies in various widely scattered areas raised some additional and striking problems in human population genetics.

Since persons who are homozygous for the sickle cell gene very rarely reproduce, there is a constant loss of sickle cell genes in each generation. In order for the gene to attain frequencies of .1 to .2, which are equivalent to about 20 to 40 percent of the sickle cell trait, there must be some mechanism which is compensating for this loss. In other words, there must be some factor which is tending to increase the number of sickle cell genes in the population. Neel (1951) first pointed out that there are two outstanding possibilities;

either the sickle cell gene is arising frequently by mutation, or the heterozygote for the sickle cell gene possesses a selective advantage over the normal homozygote which offsets the selective disadvantage of the sickle cell homozygote (balanced polymorphism). Since the evidence (Vandepitte et al. 1955) indicated that the mutation rate was not sufficient to maintain the high frequencies, selection in favor of individuals with the sickle cell trait seemed to be implicated as the factor which was maintaining them.

When Allison (1954a; 1954b; 1954c) advanced the hypothesis that the heterozygote for the sickle cell gene possessed a relative immunity to falciparum malaria, he marshalled the first clear evidence for the mechanism by which selection maintained the observed high frequencies. In addition to experiments on sicklers and nonsicklers which seemed to show that the sicklers could cope more easily with a malarial infection, Allison (1954b) also showed that the tribal frequencies of the sickle cell gene in Uganda and other parts of East Africa could be explained as well by his malaria hypothesis as by varying degrees of Hamitic admixture. Thus, Allison's work showed that selection must be taken into consideration in any attempt to explain the distribution of the sickle cell gene.

Although selection has undoubtedly played a major role in determining the frequencies of the sickle cell gene in the populations of the world, in many areas other factors in addition to selection may well be involved. Allison (1954b) has shown that most of the tribes of East Africa seem to have frequencies of the sickle cell trait which are in approximate equilibrium with the amount of malaria present, but there appear to be many populations in West Africa and elsewhere for which this is not so. It will be the purpose of this paper to show how the distribution of the sickle cell gene in West Africa is the result of the interaction of two factors, selection and gene flow. Gene flow will be used here to include both migration and mixture; the term migration is used where the gene flow involves the movement of breeding populations or large segments of them, and mixture where the breeding populations remain rather stationary and the gene flow involves the exchange of individuals between them. Of course, any actual situation is usually a combination of these two "polar" concepts.

According to modern genetic theory as developed by Wright and others, there are five factors which can contribute to gene frequency change: selection, mutation, gene drift, gene flow, and selective mating. Strictly speaking, an attempt to explain the distribution of any gene must take into consideration all five. However, three of these factors—mutation, gene drift, and selective mating—are thought to have had relatively little effect on the features of the distribution of the sickle cell gene in West Africa which this paper will attempt to explain, and thus will not be discussed at any length in this paper.

The general plan of the paper will be as follows. First, the distribution of the sickle cell gene in West Africa will be plotted; then an attempt will be made to correlate this distribution with that of falciparum malaria in West Africa. It will be assumed that the high frequencies of the sickle cell gene are

in equilibrium with the particular endemicity of malaria in which they are found. Thus, by comparing these two distributions we can determine where the frequencies of the sickle cell gene appear to be explained by selection (i.e. are in equilibrium), and we can also determine where the frequencies appear to be very far from equilibrium and hence where other factors in addition to selection appear to be involved. The rest of the paper will then be concerned with the populations which do not appear to be in equilibrium. In order to explain why the frequencies of the sickle cell gene in these populations are not in equilibrium with the present-day endemicity of malaria, it is necessary to have some idea of the ethnic and culture history of West Africa. The literature on the culture history of West Africa is rather sparse, so the major part of this paper will be an attempt to infer its broad outlines from the distribution of language and of certain domesticated plants in West Africa.

THE DISTRIBUTION OF THE SICKLE CELL GENE IN WEST AFRICA

In the following compilation of data on the distribution of the sickle cell gene in West Africa, several early publications of surveys have been omitted. In all of these reports, the tribe of the persons tested is not given, and the reports could thus contain subjects from several breeding populations with very different frequencies of the sickle cell gene. Data by tribe are available for the areas covered by these surveys, except for part of Evans' (1944) survey. His sample from the Cameroons has been included since there are no other data from this area.

Where the same tribe has been tested by different investigators, differences in the frequency of the sickle cell trait have been tested by a chi-square test. If the differences were not significant, the results have been combined. However, for several large tribes which extend over considerable distances and into several different countries, the samples have been kept separate when they were obtained in different countries.

For the surveys in which paper electrophoresis or other biochemical tests were done on the bloods, all individuals who would have been positive for the sickle cell test were counted as positive without regard to whether they appeared to be homozygous or heterozygous for the sickle cell gene. Thus, the frequency of the sickle cell trait, as used in this paper, includes both heterozygotes and any living homozygotes for the sickle cell gene. However, recent studies (Lehmann and Raper 1956) indicate that homozygotes for the sickle cell gene rarely survive the first years of life, so that most likely very few homozygotes are included in the tribal samples. Throughout the discussion, sickle cell trait frequencies will be used instead of gene frequencies, since the trait frequencies are used by most investigators and hence their significance is more easily comprehended. Since very few homozygotes are included in the samples, the gene frequency would be close to one-half the trait frequency in all cases.

Except for the Ivory Coast, Dahomey, and the Cameroons, the compilation is by tribe. The Dahomey and Cameroons samples have been included in

an effort to fill up large gaps in the distribution in areas where tribal investigations are nonexistent. These samples have combined several tribes and thus have probably combined data from isolates which differ significantly from one another in the frequency of the sickle cell trait. Since they are also quite small samples, this paper will not consider them in detail.

Due to the lack of investigations, and also to the multiplicity of small tribes which inhabit the Ivory Coast, the tribal samples from there are all rather small. Since the frequency of the sickle cell trait is 0 percent in Liberia to the west of the Ivory Coast and greater than 20 percent in Ghana to the east, the Ivory Coast is an area of crucial concern to this study. For this reason, the tribal samples have been combined into larger linguistic units to increase the sample sizes and thus give them more reliability. The tribes which have been combined are very closely related, since in most cases they speak the same language with only dialectic differences between them. Although the individual tribal samples are small, there is no indication that this procedure has combined tribes which have very different frequencies of the sickle cell trait.

Table 1 shows the frequency of the sickle cell trait for West Africa by tribe and also by country. For the purposes of further discussion, the spelling of all tribal names has been standardized. On Table 1 the names used by the original investigators are shown in parentheses after the standardized name.

The distribution of the frequency of the sickle cell trait in West Africa is shown on Figure 1. In order to make the general configuration of the distribution more easily visualized, the frequencies have been grouped into five categories: 0–2, 2–8, 8–15, 15–22, and greater than 22 percent. The frequency of the sickle cell trait can be seen to exhibit extreme variability, sometimes over very short distances. In many cases there are significant differences in the frequency of the trait even within the same tribe. For example, the Fulani have frequencies ranging from 8 to 25 percent, and the Mandingo in the Gambia vary from 6 to 28 percent. Although this great variability impedes generalizing about the distribution, some significant generalizations can nevertheless be made.

Generally, the higher frequencies tend to be toward the south, and, despite many exceptions, there is some indication of a north-south gradient in the frequency of the sickle cell trait. The distribution of falciparum malaria follows a similar gradient, and, in addition, all the populations which have sickle cell trait frequencies greater than 15 percent inhabit areas where malaria is either hyperendemic or holoendemic.

In an environment in which malaria is hyperendemic or holoendemic, the disease is transmitted throughout most of the year, so that the individuals are continually being reinfected. The average number of infective bites per person per year is always greater than about 5, and in some areas ranges up to 100 or more. Thus, infants are infected with malaria shortly after birth, and for about the first five years of life every child is engaged in a mortal struggle with the parasite. During these years the parasite rate (i.e., the percentage of individuals harboring malaria parasites) is close to 100 percent, and there is a

TABLE 1. THE FREQUENCIES OF THE SICKLE CELL TRAIT IN
THE TRIBES OF WEST AFRICA

Country Tribe	Investi-gations*	Number Examined	Number Positive	Sickle Cell Trait (%)
Senegal				
Wolof (Ouolof)	16, 18	2277	151	6.63
Lebu (Lebou)	16, 18	522	31	5.94
Serer	16, 18	1515	50	3.30
Soce	16	70	11	15.71
Fulani (Peul)	16, 18	299	27	9.03
Tukulor (Toucouleur)	16, 18	634	60	9.46
Dyola	18, 19	39	2	5.13
Mandiago	16, 18, 19	101	1	0.99
Gambia				
Mandingo-Western Division	2	167	18	10.78
Mandingo-Keneba	2	240	15	6.25
Mandingo-Jali	2	115	7	6.09
Mandingo-Manduar	2	59	10	16.95
Mandingo-Tankular	2	132	32	24.24
Fulani (Fula)	2	127	24	18.90
Dyola (Jola)	2	312	53	16.99
Wolof (Jolloff)	2	104	18	17.31
Saracole (Serahuli)	2	96	8	8.33
Bainunka	2	90	15	16.67
Portuguese Guinea				
Papel	24	500	15	3.00
Mandiago (Mandjaca)	15	500	16	3.20
Balante (Balanta)	15	500	25	5.00
Feloop (Felupe)	15	466	6	1.72
Baiote	15	473	6	1.27
Nalu	15	501	14	2.79
Saracole	15	286	24	8.39
Mandingo (Mandinga)	15	500	75	15.00
Biafada (Beafada)	15	505	77	15.25
Pajadinca	15	358	66	18.44
Fulani (Fula-Foro)	15	500	115	23.00
Fulani (Fula-Preto)	15	430	108	25.12
French Guinea				
Fulani (Foula)	15, 16, 18	682	109	15.98
Susu	5, 18, 19	48	15	31.25
Kissi	19	18	4	22.22
Loma-Kpelle (Toma-Guerze)	19	40	8	20.00
Sierra Leone				
Creole	2	42	10	23.81
Timne	2	52	15	28.95
Mende	2, 23	1124	330	29.36
Liberia				
Kissi	17	298	58	19.46

TABLE 1. THE FREQUENCIES OF THE SICKLE CELL TRAIT IN
THE TRIBES OF WEST AFRICA (Continued)

Country Tribe	Investi- gations*	Number Examined	Number Positive	Sickle Cell Trait (%)
Mende	17	77	13	16.88
Gbandi	17	352	54	15.34
Vai	17	93	13	13.98
Kpelle	17	982	128	13.03
Loma	17	511	65	12.72
Gola	17	183	22	12.02
Belle	17	29	3	10.34
Bassa	17	811	58	7.15
Dei	17	53	2	3.77
Mano	17	709	15	2.12
Gio	17	428	9	2.10
Grebo	17	69	1	1.45
Krahn	17	154	1	0.65
Kru	17	148	1	0.68
Webbo	17	77	0	0.00
French Sudan				
Moor (Maure)	18, 19	70	4	5.71
Saracole	16, 18	196	16	9.18
Bambara	16, 18	262	27	10.31
Mandingo (Malinke)	18, 19	50	8	16.00
Fulani (Peul)	20	152	22	14.47
Songhoi	20	100	11	11.00
Ivory Coast				
Senufo	5, 19	33	8	24.24
Agni-Baule	5, 19	53	7	13.21
Dan-Gnouro	5, 19	30	0	0.00
Lagoon	5, 19	48	2	4.17
Bete	5, 19	53	1	.89
Bakwe	5, 19	63	1	1.59
Upper Volta				
Samogo	20	120	8	6.67
Bobofing	5, 19, 22	232	57	24.57
Lobi	5, 19	15	3	20.00
Mossi	5, 19, 20	207	24	11.59
Gurma	5, 19, 20	34	3	8.82
Gurunsi	5, 19	14	1	7.14
Ghana				
Mossi (Moshie)	10, 11	121	5	4.13
Dagarti	11	97	11	11.34
Dagomba	11	71	3	4.23
Ewe	2, 10, 11	232	54	23.28
Fanti	2, 10, 11	204	48	23.53
Ga	2, 10, 11	367	67	18.26
Twi	2, 10	111	24	21.62
Ashanti	2	102	23	22.55

TABLE 1. THE FREQUENCIES OF THE SICKLE CELL TRAIT IN
THE TRIBES OF WEST AFRICA (Continued)

Country Tribe	Investi- gations*	Number Examined	Number Positive	Sickle Cell Trait (%)
Frafra	9	680	66	9.71
French Togoland				
Kabre	4	1104	109	9.87
Dahomey				
Dahomeans	5, 19	55	5	9.09
Niger				
Djerma (Zabrama)	2, 19	69	15	21.74
Tuareg	3	93	5	5.38
Nigeria				
Yoruba	7, 13, 25	3477	853	24.53
Igalla	25	155	28	18.06
Ibo	2	51	11	21.57
Cameroons	12	138	21	15.22
Kerikeri	14	159	17	10.69
Fulani	14	184	31	16.85
Hausa	1, 6, 14	611	107	17.51
Lake Chad				
Mohur (Mobeur)	21	273	49	17.95
Kanembu (Kanembou)	21	76	17	22.37
Mangawa	21	58	12	20.69
Sugurti (Sougourti)	21	37	6	16.22

* References are as follows:

1—Adamson (1951)
2—Allison (1956)
3—Barnicot, Ikin, and Mournat (1954)
4—Bezon (1955)
5—Binson, Neel, and Zuelzer (unpublished)
6—Bruce-Chwatt (unpublished)
7—Charles and Archibald (unpublished)
8—Colbourne, Edington, and Hughes (1950)
9—Colbourne and Edington (1956)
10—Edington and Lehmann (1954)
11—Edington and Lehmann (1956)
12—Evans (1944)
13—Jelliffe and Humphreys (1952)
14—Jelliffe (1954)
15—Leite and Ré (1955)
16—Linhard (1952)
17—Livingstone (1957b)
18—Neel, Hiernaux, Linhard, Robinson, Zuelzer, and Livingstone (1956)
19—Pales and Linhard (1951)
20—Pales and Serere (1953)
21—Pales, Gallais, Bert, and Fourquet (1955)
22—Raoult (unpublished)
23—Rose and Suliman (1955)
24—Trincao, Pinto, Almeida, and Gouveia (1950)
25—Walters and Lehmann (1956)

considerable mortality from the disease. Those individuals who survive this struggle have a solid immunity to malaria. In later years they are being continually reinfected with malaria but are able to keep their infection at a subclinical level. The parasite rate then decreases among older children and is lowest in adults. In holoendemic malaria the adult parasite rate will be about 20 percent and the adults will almost never have any clinical symptoms of malaria, while in hyperendemic malaria the adult parasite rate will be some-
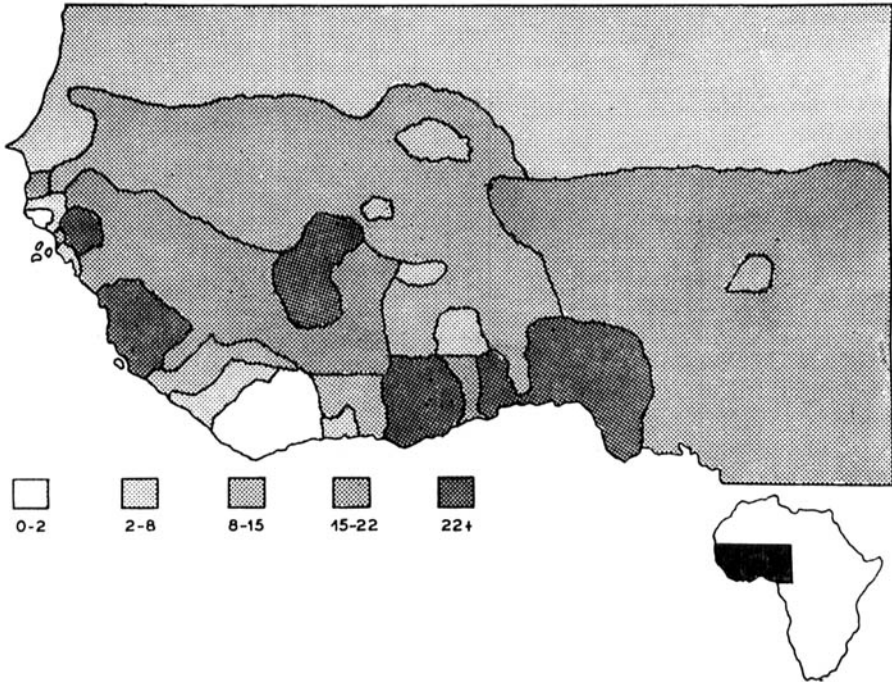
FIG. 1. The distribution of the frequency of the sickle cell trait in West Africa.

what higher and the adults will sometimes have clinical symptoms, usually chills and fever. However, in both these conditions there is seldom any adult mortality from malaria.

It is in an environment in which malaria is either hyperendemic or holoendemic that the heterozygote for the sickle cell gene has been postulated to have a selective advantage over the normal homozygote. Allison (1954a) and Raper (1955) have shown that, although sicklers are infected with falciparum malaria almost as readily as nonsicklers, in the younger age groups the very high densities of parasites are not found as often among sicklers. In addition, Raper (1956) has shown that the sicklers do not suffer from cerebral malaria and blackwater fever as much as nonsicklers. Since these are the complications of falciparum malaria which result in death, the sicklers had a lower mortality rate from falciparum malaria. In addition, I have postulated (1957a) that if

the sickling females did not have as heavy falciparum infections of the placenta as did normal females, they would have a higher net reproduction rate and hence this could be another mechanism by which malaria was maintaining the high frequencies of the sickle cell gene. Although the evidence is not conclusive, it seems for the most part favorable to this hypothesis. When the evidence for both these mechanisms is considered as a whole, it seems to be conclusive that malaria is the major cause of the high frequencies of the sickle cell gene. One would therefore expect to find high frequencies of the sickle cell trait in areas in which malaria is either hyperendemic or holoendemic.

From about the latitude of the Gambia south, West Africa is almost entirely characterized by hyperendemic or holoendemic malaria; hence, high frequencies of the sickle cell trait would be expected. However, there are many populations in this region with very low frequencies of the trait. The majority of them are found in three areas: (1) Coastal Portuguese Guinea, (2) Eastern Liberia and the Western Ivory Coast, (3) Northern Ghana. The low frequency populations which are found in Northern Ghana differ from those in the other two areas by having high frequencies of the gene which is responsible for Hemoglobin C. This gene is an allele of the sickle cell gene (Ranney 1954), so that in Northern Ghana the sickle cell locus is a tri-allelic system. Since the selective values associated with the various phenotypes of this system are not known at present, the equilibrium frequencies for these populations cannot be ascertained (see Allison 1957 for further discussion of this problem). Thus, one cannot say whether or not these populations are in equilibrium for this locus. The rest of this paper will therefore be concerned with the two areas, Coastal Portuguese Guinea and Eastern Liberia-Western Ivory Coast, where the Hemoglobin C gene is almost completely absent (Neel et al. 1956).

Cambournac (1950) in Coastal Portuguese Guinea and Young and Johnson (1949) in Eastern Liberia found malaria to be either hyperendemic or holoendemic in these areas where low frequencies of the sickle cell trait are found. Thus, these frequencies appear to be very far from equilibrium, and hence do not seem to be explained by the factor of selection alone. An attempt will now be made to show how the explanation involves the two factors, selection and gene flow. More specifically, two hypotheses will be advanced to explain these low frequencies:

(1) The sickle cell gene has been present in some parts of West Africa for a considerable time, but, due to the comparative isolation of the low frequency populations in Portuguese Guinea and Eastern Liberia, is only now being introduced to them.

(2) The environmental conditions responsible for the high frequencies of the sickle cell gene have been present for a relatively short time among these populations, so that the spread of the sickle cell gene is only now following the spread of the selective advantage of the gene.

In order to demonstrate these propositions, two general types of evidence will now be considered; first, the distribution of language in West Africa, from which an attempt will be made to ascertain the general outlines of the migra-

tions which have occurred there; then, the archeological evidence and the distributions of certain domesticated plants in West Africa, from which an attempt will be made to determine the broad outlines of the culture history of the area. From a consideration of the culture history of West Africa and the relationship between culture patterns and the endemicity of malaria, the spread of the selective advantage of the sickle cell gene will be inferred.

THE DISTRIBUTION OF LANGUAGE IN WEST AFRICA

In the following discussion Greenberg's (1955) classification of African languages will be used, since it is the most recent and also the most widely accepted. In addition, Greenberg is attempting to make a "genetic" classification of African languages. Languages are said to be genetically related when their similarities are due to their development from a common ancestral language. It is this type of linguistic relationship which is most likely to have biological significance, since the ancestors of the speakers of genetically related languages were probably once members of the same breeding population and thus biologically related. Greenberg's classification is concerned with the larger linguistic families of Africa and the larger subgroupings within these families. Since it will be necessary at times to separate the languages into smaller subgroups, other sources will be used, but only when these agree with Greenberg's overall classification.

Except for the Songhai, Hausa, Kerikeri, Tuareg, Moor, and the tribes around Lake Chad, all the tribes listed on Table 1 speak languages belonging to the Niger-Congo family. The exceptions noted above speak either Songhai, Central Saharan, or Afro-Asiatic languages. These tribes are in the northern and eastern parts of West Africa and a considerable distance from the two low frequency areas of the sickle cell trait with which we are concerned. Therefore, this discussion will be concerned only with the Niger-Congo languages.

Figure 2 shows the language distribution in West Africa, both by family and by subfamily within Niger-Congo. The Niger-Congo family contains seven subfamilies: (1) West Atlantic, (2) Mande, (3) Gur, (4) Kwa, (5) Central Group, (6) Ijo, (7) Adamawa-Eastern. All of these subfamilies have some member languages in West Africa, but, with the exception of the Adamawa-Eastern speakers in northern Central Africa, the Niger-Congo languages in Central, East, and South Africa all belong to a single subfamily (Central Group) and even to a single subgroup (Bantu) within that subfamily.

Because of the great linguistic diversity in West Africa, this area appears to have been inhabited for a relatively long time by speakers of Niger-Congo. On the other hand, because of the similarity of language in the area inhabited by the Bantu peoples, this area has undoubtedly been peopled by a relatively recent spread of those peoples. As Greenberg (1955:40) states:

If the view of the position of the Bantu languages presented here is accepted, there are certain historical conclusions of considerable significance which follow. When Sapir demonstrated that the Algonkian languages were related to the Wiyot and

Yurok languages of California, it was clear that, if this demonstration was accepted, it constituted a powerful argument for the movement of the Algonkian-speaking peoples from the west to the east. Here we have not two languages, but twenty-three separate stocks all in the same general area of Nigeria and the Cameroons. The evidence thus becomes strong for the movement of the Bantu-speaking peoples from this area southeastwards. The usual assumption has been a movement directly south from the great lake region of East Africa. It will also follow that this is a relatively recent movement, a conclusion which has generally been accepted on the basis of the
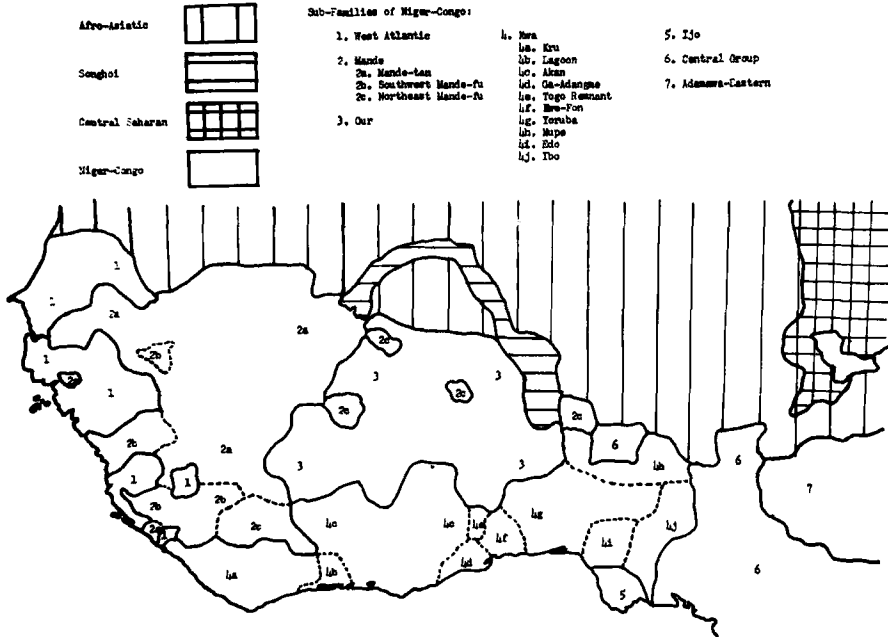
FIG. 2. The distribution of language in West Africa.

wide extension of the Bantu languages and the relatively small differentiation among them.

In discussing the archeological and ethnological evidence, an attempt will be made to give reasons for the relatively recent spread of the Bantu from Nigeria, as well as to show that this other evidence seems to support the linguistic evidence.

In West Africa west of Nigeria, there are four subfamilies of Niger-Congo: West Atlantic, Mande, Gur, and Kwa. With the exception of the rather recent movement of the Fulani pastoralists across the entire length of West Africa, the West Atlantic languages are all located along the coastal fringe of West Africa. The Kwa languages are distributed along the Guinea Coast from Liberia to Central Nigeria, with the great majority of them located in the tropical rain forest. In the central part of West Africa, in two large blocks, are the Mande languages on the west and the Gur languages on the east. These

languages are for the most part located in the sudan, although several Mande groups have penetrated the tropical rain forest in Sierra Leone, Liberia, and the Ivory Coast.

The tribes with low frequencies of the sickle cell trait in Portuguese Guinea speak West Atlantic languages, but some Mandingo groups in the Gambia, who speak a Mande language, also have relatively low frequencies. In Eastern Liberia and the Western Ivory Coast, the tribes with low sickling frequencies include speakers of Kwa and Mande languages. Thus, with the exception of Gur, all these subfamilies include some languages whose speakers are far from equilibrium with respect to the sickle cell gene. Since these subfamilies also include some languages whose speakers have high frequencies of the sickle cell trait and seem to be close to equilibrium, the frequency of the trait is not correlated with language. This seems to indicate that the gene has been introduced into this part of West Africa since these subfamilies of Niger-Congo began to separate. However, since there is considerable linguistic diversity within the subfamilies, their separation occurred long ago.

Although there is no correlation of the frequency of the sickle cell trait with the linguistic subfamilies in this part of West Africa, the tribes with low frequencies in both Portuguese Guinea and Eastern Liberia seem to be the indigenous inhabitants of West Africa who have been forced back into these areas by later migrants from the east. The distribution of the West Atlantic languages along the coast with some isolated pockets in the interior indicates that the speakers of these languages were once more widespread and have been forced back to the coast by more recent invaders (Forde 1953). This retreat of the West Atlantic speakers is documented to some extent, and there is general agreement that the general trend of migration has been toward the west. Of course, the West Atlantic peoples probably occupied the coastal regions at an early time also, but their present concentration there results from their displacement from a wider area by invaders from the east.

Several authorities state that the Baga, who now inhabit the coastal regions of French Guinea, originally inhabited the Futa Djallon, which is the highland area of Central French Guinea. The Baga were forced out of there by the Susu, who were in turn forced out by the Fulani (Houis 1950; Demougeot 1944; Joire 1952). This forcing back of the West Atlantic speakers was also noted by Beranger-Ferand (1879:285) in the Casamance River area of the French Senegal. He divides the populations of this region into three groups:

A. Peuplades primitives (Feloupes, Bagnouns).
B. Peuplades envahissantes (Balantes, Mandingues, Peuls).
C. Peuplades adventives (Ouolofs, Saracoles, Toucouleur, Mandiagos, Machouins, Taumas, Vachelons).

He then states that A are the indigenous inhabitants; B are the fighters who conquered; and C are the traders or farmers who infiltrated in small groups. In Gambia the same migrations have been noted by Southorn (1952) and Reeve (1912). Reeve (1912:17) states:

The only relics that are to be found today of the primitive negro race which orig-

inally occupied the forest belt between the Senegal and the Rio Grande are the Serreres on the coast, north of the Saloum River, who are pagans and were cannibals; the Feloops, Floops, or Flups, as called by early voyagers, but now, in the valley of the Gambia, known as the Jolahs, occupying the territory between the seacoast and the headwaters of the Vintang Creek, about one hundred miles inland; the Patcharis or Pakaris in the Middle Valley, and the Bassaris including the Kunyadis, in the Upper Valley. These will be again referred to, and it is evident, from the chronicles of the different writers on the subject of slavery in this part of West Africa, that it was these Arcadians and forest dwellers, with their simple manners and customs of sustaining life from the products of the forest, field, and streams, who supplied the bulk of the trade, under the pretext that they worshipped idols, and therefore were considered to be outside the pale of humanity by the races that had adopted the Koran.

Thus, it can be seen that these writers agree that the Feloops, who have one of the lowest frequencies of the sickle cell trait, are one of the indigenous tribes. In addition, Reeve states that the Serer, who also have a low frequency of the trait, are the indigenous inhabitants in the north and in the past were hunters and gatherers and not agriculturalists. It should also be noted that Leite and Ré (1955), who tested the tribes of the Portuguese Guinea for sickling, give a similar explanation for the differences in the frequency of the sickle cell trait which they found.

The tribes with low sickling frequencies in Eastern Liberia and the Western Ivory Coast include speakers of Mande languages and of Kwa languages. All of the speakers of Kru and Lagoon languages, which belong to the Kwa subfamily, have very low frequencies of the sickle cell trait, and the positives for the trait who do occur among these peoples are in the eastern tribes where they are in contact with the Agni, Baoule, and other Akan speakers. On the other hand, the Kwa speakers who are to the east of the Kru and Lagoon peoples all have relatively high frequencies of the sickle cell trait. Viard (1934) states that the Guere, who speak a Kru language, came from the east, and Yenou (1954) makes a similar statement for the Alladians, who speak a Lagoon language. Since the linguistic relationships point to the east, these statements are probably true. Much has been written about the migrations of the Akan, Ewe, Ga, and other Kwa speakers who are to the east of the Kru and Lagoon speakers, and most authorities agree that the general direction of migration of these tribes has been to the southwest. Since the Lagoon languages are quite similar to the Togo Remnant languages (Bertho 1950), it seems that the speakers of these languages were forced back into peripheral areas by the Akan peoples (i.e., Ashanti, Fanti, Agni, Baoule), when they migrated to Southern Ghana. The movement of the Agni and Baoule into the Ivory Coast is quite recent—17th century according to most authorities. Thus, it seems that some Kwa speakers were more widespread through the tropical rain forest when the later Kwa migrants entered it and were then forced back by these later migrants. Since the later migrants have high frequencies of the sickle cell trait, it appears that they introduced the sickle cell gene into this part of West Africa.

In addition to the Kru and Lagoon-speaking peoples, there are several

tribes with low sickling frequencies who speak Mande languages in Eastern Liberia and the western Ivory Coast. These are the Mano, Gio, Dan, Gouro, and other smaller groups. At the border between the Mano and the Kpelle, the frequency of the sickle cell trait increases sharply. Although these peoples both speak Mande languages, they belong to different subgroups of the Mande subfamily (Prost 1953). Kpelle is related to Mende and Susu to the northwest in Sierra Leone, and this tribe has undoubtedly come into Liberia from that direction. However, Mano and the other Mande languages whose speakers have low-frequencies of the sickle cell trait are related to several Mande languages in the Upper Volta Province of French West Africa and also to a Mande language in Nigeria. Vendeix (1924) states that the Dan, and Tauxier (1924) that the Gouro, came into their present habitats from the northeast. Donner (1939) states that the Dan came from the north into the forest and forced the Kru peoples ahead of them. It would thus appear that these Mande tribes with low sickling frequencies came into their present location by a different route than that of their Mande neighbors to the northwest in Liberia and Sierra Leone. The Bobofing, who speak a language related to these Mande languages whose speakers have low sickling frequencies, have 25 percent of the sickle cell trait and are some distance to the northeast of the Dan and Gouro; so that it seems that the sickle cell gene was introduced after the separation of these languages. The Mandingo are to the north of the Mano, Dan, and Gouro, and between them and the Bobofing. From the 12th to 15th centuries A.D. when the Mali Empire, which was ruled by the Mandingos, was at its height, these people are known to have expanded out from their original homeland. It would appear that this expansion of the Mandingo forced the Mano, Dan, and Gouro into the forest and separated them from their relatives to the northeast.

The two areas of low frequencies of the sickle cell trait thus seem to be inhabited by peoples who have been forced back into these peripheral areas by later migrants from the east and northeast. However, this does not mean to imply that all the later migrants had the sickle cell gene. It is possible that the Kwa migrants to Southern Ghana introduced the gene into this part of West Africa by migration; but along the West Atlantic coastal fringe, the sickle cell gene seems to have spread in the past by mixture, and is still spreading in this manner today.

In the Central Ivory Coast on the border of the Kru and Lagoon peoples on the west and the Akan peoples on the east, there is a sharp increase in the frequency of the sickle cell trait. Since all the Kwa peoples from the Akan east to the Ibo in Nigeria have very high frequencies of the trait, it seems that these peoples possessed the sickle cell gene when they migrated into these regions from the east and northeast. However, along the Atlantic Coast of West Africa from the Senegal to Central Liberia, the gene does not seem to have been introduced by large-scale migration. The highest frequencies of the sickle cell trait in this region are found in the Gambia and in Sierra Leone, which are also the two places where Mande peoples have penetrated to the

seacoast in large numbers. Since the Mande peoples were the migrants from the east, it would appear that they introduced the sickle cell gene into this part of Africa. However, the smooth gradient in the frequency of the trait in Sierra Leone and Liberia seems to indicate that the gene was introduced after the original Mande migrations. Starting with the Susu in northwest Sierra Leone who have a sickling frequency of 31 percent and proceeding southeast-ward, there is a smooth gradient in frequency which is not correlated with language. The speakers of Southwest Mande-fu languages, the Mende in Sierra Leone, the Mende in Liberia, the Gbandi, Loma, and Kpelle, have 29, 17, 15, 13, and 13 percent, respectively, while the West Atlantic speakers, the Timne, Kissi, and Gola, have 29, 19, and 12 percent respectively. The Vai, who speak a Mande-tan language and are the latest immigrants from the interior (McCulloch 1950), have a frequency of 14 percent, which is also in agreement with this gradient. In Portuguese Guinea, where the Mande peoples have not penetrated in great numbers, there is also a smooth gradient in the frequency of the sickle cell trait. Starting on a small section of the seacoast between the Casamance River and the Rio Cacheu where the Feloop and Baiote have 1 to 2 percent, the frequency increases going inland to 5 percent among the Mandjak, and then to 15 percent among the Biafada and Mandingo. It thus seems that along the West Atlantic coastal fringe of West Africa the sickle cell gene has spread and is still spreading by mixture and not by large scale migration, while the gene appears to have spread through the tropical rain forest along the Guinea Coast by the migration of the Akan and other Kwa-speaking migrants from the east. The archeology and culture history of West Africa will now be examined in an attempt to provide some explanation for the manner by which the sickle cell gene has spread there.

THE ARCHEOLOGY OF WEST AFRICA AND ORIGIN OF THE WEST AFRICAN NEGRO

Although there has been less archeological excavation in West Africa than elsewhere in Africa, it is now beginning to appear that West Africa was in-habited during most of man's cultural development, as was most of the con-tinent. Lower Paleolithic hand axes and Middle Paleolithic Levallois flakes have been found in scattered places throughout West Africa (Alimen 1955). However, no rich sites comparable to those in East and South Africa have been excavated for these stages. Nevertheless, the scattered finds indicate the pres-ence of man in West Africa during these periods, which lasted up to the end of the Pleistocene. Following these periods in time, microlithic sites are docu-mented for Ghana (Shaw 1951), French Guinea (Joire 1952), Nigeria (Fagg 1951), and other places in West Africa. Some of these microlithic cultures seem fairly recent and perhaps attributable to the ancestors of the present Negro inhabitants. However, little skeletal material has been found.

The earliest skeletal material which is found close to West Africa is a skull from Singa in the Sudan. This find has been dated by Arkell (1952) as Upper

Pleisetocene and is associated with a Levallois culture. The skull is stated to be archaic Bushman and related to the Boskop skull from South Africa. From this find it appears that the Bushman was once much more widespread than today and in Upper Pleistocene times Bushman-like peoples were in the Sudan. This statement is supported by the presence of Bushman-like rock paintings and archeological cultures similar to that of the present day Bushman over most of the southern half of the African continent. The presence today in Tanganyika of the Hatsa, who speak a Khoisan language and still have a predominantly Stone Age culture (Fosbrooke 1956), also supports it.

The first appearance of skeletal material which has Negroid affinities is in this same area of the Sudan, but apparently much later. At Esh Shaheinab, which is on the Nile near Khartoum, several skeletons with Negroid affinities have been found in association with a microlithic hunting and gathering culture, which also had pottery. Around the fringes of the Sahara there are other finds of Negroid skeletal material, all of which seem to belong to this general period. The famous Asselar skull from north of Timbuktu, which is considered to be Negro, is from this general period, and Alimen (1955) also indicates that some of the skeletal material associated with the Capsian culture in Tunisia has Negroid affinities. In addition to this skeletal material, many of the early rock paintings in the Sahara seem to depict Negroid peoples.

The Esh Shaheinab site has been dated by radiocarbon as 5200 years ago, or shortly after the beginnings of agriculture in Egypt. The radiocarbon dates on the Capsian culture are about 7500 years ago. Alimen (1955) indicates that the Neolithic of Capsian tradition is found in French Guinea, but this is probably much later than the Capsian sites which have been dated by radiocarbon. It should also be noted that in this context Neolithic does not mean food-producing, but only that the culture had polished stone artifacts.

The first archeological evidence of the Bantu in South and Central Africa is much later than the evidence from northern West Africa, and appears to be after the beginning of the Christian era. Alimen (1955:304) states: "Iron entered the Congo very late, by means of the Bantu invasion, which later spread to the Rhodesias in only 900 A.D." Further, Alimen states (1955:370) that ironworking came to the upper valley of the Orange River in the 13th century A.D. and here too is associated with the arrival of the Bantu. Previous to the expansion of the Bantu, East and South Africa were inhabited by Bushman-like peoples.

The archeological evidence thus seems to indicate that at about the time of the introduction of agriculture into Africa, Negro peoples with a microlithic culture were living around the fringes and even in the middle of the Sahara, while most of South and East Africa was inhabited by Bushman-like peoples. Since the Pygmies would seem to be indigenous to Central Africa, they were perhaps responsible for the microlithic cultures found there. For West Africa there are numerous legends of Pygmies (summary in Schnell 1948), so it is possible that at this time Pygmies also inhabited West Africa. However, Joire (1952) thinks there is no evidence for Pygmies in West Africa and assigns the

microlithic sites in French Guinea to the Baga tribe. The diffusion of agriculture through Africa, and its effect on the preceding distribution of peoples will now be considered.

THE INTRODUCTION OF AGRICULTURE AND IRON WORKING INTO AFRICA

The first evidence of a farming economy in Africa occurs in Egypt at Fayum, which dates about 4000 B.C. Because of the domesticated plants and animals associated with this culture, it is thought to be derived from Asia Minor (Alimen 1955). Seligmann (1939:52) shows instances of Egyptian contact with Negroes in the late predynastic period, which he dates at about 3000 B.C., and Negroes are also known to have been living in the Sudan at Esh Shaheinab at about the same time. The inhabitants of Jebel Moya in the Sudan are also stated to be Negroes, who were forced westward by the Arabs around 700 B.C. (Mukherjee, Rao, and Trevor 1955). Thus, agriculture seems to have spread from Egypt to the Negro peoples who have since been forced south and west by the Arabs and by Berber peoples such as the Tuareg.

Iron working was also introduced into Africa from Asia Minor via Egypt (Forde 1934; Arkell 1955). There was a considerable iron industry flourishing at Meroe in the Sudan in 600 B.C., about which Arkell (1955:147) states: "Indeed there is little doubt that it was through Meroe that knowledge of iron working spread south and west throughout Negro Africa." The next evidence for the spread of iron southwest of the Sudan is in Northern Nigeria where Fagg (1956) has discovered the Nok culture, which is dated in the second half of the first millennium B.C. by geological methods. Assuming that iron working spread here from Meroe, this is about the date which would be expected. This culture contains both iron and stone axes; but since the iron axes have the same shape as the stone ones, this appears to be a transitional culture which had only recently adopted iron working. Since Mukherjee, Rao, and Trevor (1955) found the inhabitants of Jebel Moya to be most similar in physical type to the West African Negro, the westward migration of these people in the first millennium B.C. could very likely have been the method by which iron working was introduced to West Africa. In any case, this appears to be one route by which iron working was introduced into West Africa.

In the western part of West Africa, iron working seems to be somewhat later, and the evidence seems to indicate that it was not introduced via Meroe. Corbeil, Mauny, and Charbonnier (1948) think that iron working was introduced into the Cape Verde region around Dakar by Berbers who arrived there from the north about 300 B.C. Later, Mauny (1952) states that iron working was introduced into this region by the Phoenicians in the first century A.D., since the words for iron in many of the languages of this region seem to be derived from Phoenician. Although it is possible that some peoples along the coast obtained iron from the Phoenicians, it would seem more likely that iron working was brought across the Sahara, since contact with the Phoenician ships would not seem to have been close enough for the transference of all the

techniques which iron working requires. Cline (1937) states: "Within the bend of the Niger lies the only large area where iron remains have been found associated with stone-using cultures." However, Nok culture in Northern Nigeria had not been discovered at the time Cline was writing, so that there appear to be two areas with these transitional cultures. In the same area Cline (1937) describes another type of iron working site which has copper and a much richer assemblage altogether. These sites he associates with the Ghana Empire. This empire was founded about 300–400 A.D. (Fage 1955), at about the time the camel was introduced into the western Sahara, and its rise to eminence is associated with increasing trade with Mediterranean civilizations. It thus appears that iron working was introduced into the western part of West Africa shortly before this empire was founded and probably was introduced from the north across the desert.

The preceding evidence indicates that both agriculture and iron working were introduced into West Africa from Asia Minor via Egypt, although both were no doubt diffused along several different routes. Agriculture was present in Egypt centuries before iron working and probably began to spread through Africa before iron working was introduced from Asia Minor. However, this early spread of agriculture seems to have been mostly by stimulus diffusion, since the basic crops of Egypt, wheat and barley, did not spread to the Sudan. Even today, millet and sorghum are the basic crops throughout the Sudan. Both millet and sorghum, or at least some species of them, are considered to have been domesticated in Africa (Miege 1951; Viguier 1945) and to have been cultivated there ·"since antiquity" (Miege 1951). Viguier (1945:165) states: "Aug. Chevalier considers the western sudan and its saharan border as one of the centers of the origin of domesticated sorghum." Since the agricultural methods used for them are similar to those for wheat and barley, and in addition the crops are all grains, it would seem reasonable to postulate that an early spread of agriculture from Egypt involved these crops. The techniques involved in the cultivation of these grains did not entail any considerable technological change from that of a microlithic hunting and gathering culture. The tool assemblage at Fayum in Egypt is not very different from that of the Natufian in Palestine or that of the Capsian. As this early agricultural economy spread, it either drove the hunting cultures before it or perhaps was adopted by these peoples. However, one of the hypotheses of this paper is that this economy could not spread throughout tropical Africa.

Although a Neolithic millet and sorghum economy could spread through the sudan, it was not until the introduction of iron working and/or better yielding tropical crops that the Negro agriculturalists could exploit the tropical rain forest. Thus, the forest remained the home of primitive hunters until quite recently. In West Africa these hunters appear to have been Negroes whose descendants can be seen today in the low sickling frequency areas of Portuguese Guinea and Eastern Liberia; and in Central Africa they were Pygmies, whose descendants are the low sickling frequency "true" Pygmies, the Babinga of French Equatorial Africa (Hiernaux 1955).

A combination of three factors prevented the spread of this agricultural economy through the tropical rain forest: (1) the poor quality of the soils, which wear out after a few crops; (2) the difficulty of clearing the forest with stone tools; and (3) the low yields of millet and sorghum.

In Northern Ghana and Northern Nigeria, where millet and sorghum are still the basic crops today, in many places the same fields are cultivated year after year (Manoukian 1952; Gourou 1950). On the other hand, in Sierra Leone a new field is cleared every year (McCulloch 1950), and in the forest regions of Nigeria, Gourou (1950) states that it takes 30 years for the soil to recover after one crop, while Forde (1951) indicates that the fields are cultivated for three or four years before being left fallow. Some comparison of the relative yields of the various crops can be obtained from Gourou's (1950:39) figures of yields in the French Sudan, although this is not tropical rain forest. Millet yields 5 cwt. per acre; yams, 15 cwt. per acre; and cassava, 32 cwt. per acre. However, from a nutritional standpoint the important yield is the number of calories per unit of land. Combining data from several African countries, Brock and Autret (1952) give the following figures for the yields of various crops in thousands of calories per hectare: millet yields 1,530; sorghum, 1,854; yams, 3,554; and cassava, 7,090. Thus, when these three factors are considered together, it would seem to be difficult for a Neolithic millet and sorghum economy to exist in a tropical rain forest environment. It should be emphasized, however, that this hypothesis does not mean to imply that there were no agriculturalists in the tropical rain forest prior to the introduction of iron working and tropical root crops. There was undoubtedly some agriculture and "whittling away" at the tropical rain forest in the areas which border on the sudan. However, these innovations were a necessary prerequisite for the great explosion of the Bantu peoples out of Nigeria, which filled up half a continent in a relatively short time.

Together with iron working, the domestication of two indigenous crops opened the tropical rain forest as a habitat exploitable by the Negro agriculturalists. Chevalier (1952:16) states that the yam, *Dioscorea latifolia*, was domesticated in West Africa. Today the most widespread species of yam in Africa is *D. cayenensis*, which is derived from *D. latifolia* (Chevalier 1946). From its distribution it would seem most probable that these yams were domesticated in Nigeria. With the yam and iron working, the Bantu peoples then spread throughout the Central African tropical rain forest from their original homeland, which Greenberg (1955:116) places in the central Benue River valley in Nigeria. In many places today the Bantu do not have the yam as a staple crop, but this theory only attempts to explain the original rapid spread of the Bantu. This theory is supported by linguistic evidence, by the fact that transitional iron working cultures are known in Northern Nigeria, and also by the fact that the spread of iron working in Central and South Africa is associated with the spread of the Bantu. In addition, in several areas where yams are no longer the Bantu staple there is still ritual associated with this crop, which seems to indicate that it was previously more important. For

example, among the Kpe in the Cameroons, where cocoyams are now the staple crop, Ardener (1956:46) states: "Although subsidiary in Kpe agriculture, this crop [i.e. yam] is remarkable for the fact that it is the only one to which some degree of ritual is attached. . . . The ritual elements in the cultivation of the yam, the present economic importance of which is quite small, suggests that this crop . . . may have been a staple food in the past history of the Kpe."

Also from Nigeria, some of the Kwa peoples spread in similar fashion through the West African tropical rain forest to the Ivory Coast and forced other Kwa peoples, the Kru and Lagoon speakers, westward into the Ivory Coast and Liberia. The Kru and Lagoon peoples were probably in the tropical rain forest as hunters and gatherers prior to this spread of agriculture. Agriculture has since been introduced to most of the Kru and Lagoon peoples, but it usually has rice as the basic crop, which comes from a different center of dispersal, or manioc, which was introduced into West Africa from the New World. Even today in the Ivory Coast, as several botanists (Miege 1953; Chevalier 1952) have remarked, there is a sharp boundary of yam cultivation on the Bandama River, which is also the border between the Baoule and Kru peoples. In addition, the yam cultivators, such as the Agni, have an elaborate ritual associated with the yam harvest (Rahm 1953; Miege 1953), which indicates great reliance on this crop. Although the Kru peoples have for the most part adopted agriculture, there is still more reliance on hunting in the Kru area (Kerharo and Bouquet 1949), and there are some groups who are still mainly hunters. In Eastern Liberia, Schwab (1947:79) states: ". . . there is one clan or small tribe . . . living to the north of the Tchien near the Nipwe River who have a reputation as elephant hunters, like the pigmies of the southeastern Cameroun."

The cline in the frequency of the sickle cell trait coincides with this spread of yam cultivation. The Kru and Lagoon peoples have almost 0 percent of the sickle cell trait, except where they come in contact with the yam cultivators, while the yam cultivators in the Eastern Ivory Coast, Southern Ghana, and Nigeria all have high frequencies of the trait. Thus, it seems that the sickle cell gene was brought into this part of Africa by the migrations of the yam cultivators westward from Nigeria, and at present both agriculture and the sickle cell gene are spreading to the hunting populations, which were in the forest prior to the spread of yam cultivation.

Perhaps a little later than this spread of yam cultivation, there was another spread of agriculture through the West African tropical rain forest. Porteres (1949) has shown that somewhere around the Middle Niger River Valley, a wild African species of rice, *Oryza glaberrima*, was domesticated. He dates this domestication at about 1500 B.C. (ibid.:560), but the spread of this crop through the tropical forest seems to be much later than the postulated date, and even later than the introduction of iron. There is evidence (Little 1951:26) that the first Mande peoples to enter the tropical rain forest were hunters. Little dates this migration at least 400 years ago. However, the most plausible

date seems to be about 1300 A.D., when the Susu appear to have migrated to French Guinea from the Middle Niger region (Joire 1952). Thus, it would seem that the Mande and West Atlantic peoples in the tropical forest were still hunters about 600 years ago, and that rice agriculture has since been introduced to them. Joire (1952) assigns the microlithic archeological sites which are known in French Guinea to the Baga people, who speak a West Atlantic language. These people thus were in the tropical forest prior to the immigration of the Mande peoples and to the later spread of rice agriculture.

The spread of iron working and rice cultivation through this part of the West African tropical rain forest, after the original Mande migration, does not seem to be associated with any large scale migration; it probably occurred by diffusion, since the Mande peoples who have now adopted rice cultivation were in the same location as hunters. Thus, according to the evidence, the spread of rice agriculture by diffusion seems to coincide with the spread of the sickle cell gene by mixture. In addition, the spread of rice cultivation appears to be later than the original Mande migration, as does the spread of the sickle cell gene. Rice cultivation also diffused to the West Atlantic-speaking peoples, as did the sickle cell gene. Thus, the type of gene flow—in one case migration and in the other mixture—which was responsible for the spread of the gene in West Africa seems to be related to the manner of the spread of agriculture. However, agriculture seems to have spread farther than the gene. The Kru peoples in Eastern Liberia, and the West Atlantic peoples in coastal Portuguese Guinea, are today rice cultivators. The reason for this lag in the spread of the sickle cell gene is due first of all to the fact that it takes several generations for the gene to build up to appreciable frequencies, but it also seems to be due to the relationship of the selective advantage of the sickle cell gene to slash and burn agriculture. This relationship is due in turn to the complex epidemiology of malaria in West Africa, which we will now consider.

MAN, MALARIA, AND MOSQUITO IN WEST AFRICA

In West Africa the relationship between man, malaria, and mosquito is very highly evolved, due largely to the habits of the major vector of malaria, *Anopheles gambiae*. This mosquito is attracted to human habitations and usually rests in the thatched roofs of an African village. It bites man regularly, and breeds in a variety of places. Wilson (1949) has estimated that 75 percent of the malaria in Africa is due to *A. gambiae*. Its breeding places are so diverse that, when attempting to delimit them, entomologists usually state where it cannot breed. *A. gambaie* cannot breed in (1) very shaded water, (2) water with a strong current, (3) brackish water, (4) very alkaline or polluted water (Holstein 1953).

If we now consider the types of water which would be found in the tropical rain forest, it can be seen that there would be few places for *A. gambiae* to breed in unbroken tropical rain forest. The high emergent shade trees and the trees of the middle "story" of the forest so effectively shade the ground that there would be few, if any, areas that were unshaded. In addition, the layer

of humus on the forest floor is very absorbent, so there would be few stagnant pools. It is only when man cuts down the forest that breeding places for *A. gambiae* become almost infinite (De Meillon 1949). First, with continued cutting of the forest, the soil loses all of its humus and becomes laterized. At this stage it is practically impervious to water; puddles are constantly renewed by the frequent tropical rains and so persist indefinitely. Second, man's refuse and his villages provide more abundant breeding places for the mosquito. Third, the swamps become open and hence possible breeding places.

In a hunting population, which does not destroy the forest, malaria would thus not develop this complex relation with man. Malaria could still be present, but not the holoendemic malaria which characterizes most of Africa today. Hunters do not build the type of permanent habitation in which *A. gambiae* lives, and since a hunting population moves frequently the mosquito could not keep up with the human population, so to speak. Also, in the epidemiology of any disease there is a critical size for the population below which the disease cannot persist. Since hunting populations are small, they would be closer to this critical size and perhaps even below it.

The Pygmies provide an example of such a hunting population, but unfortunately no malaria surveys of hunting Pygmies are available. Schwetz, Baumann, Peel, and Droeshant (1933) did examine three groups of Pygmies for malaria and found that they had less than the surrounding Negroes, but these Pygmies were building houses and farming, and so cannot be considered a hunting population. Putnam (1948), who lived with the hunting Pygmies for 20 years, states that they do not suffer from malaria. His account also shows that the Pygmies do not cut down the forest and do not build their rude huts in a clearing but in the middle of the forest. These customs would appear to be the reasons for the absence of malaria among them.

If this complex relationship between parasite, host, and vector which is characteristic of holoendemic malaria could not have developed in hunting populations, then the selective advantage of the sickle cell gene would not be present in these populations. If, as has been postulated, the Feloop and other peoples in Portuguese Guinea and the Kru peoples of Eastern Liberia and the Western Ivory Coast were the last remnants of hunting populations which once were spread through the tropical forest, then the absence of the selective advantage of the sickle cell gene in these populations would have prevented it from becoming established, even if there had been some gene flow from neighboring Sudanic peoples. Although considerable areas of tropical rain forest are shown on any vegetation map of West Africa, these are greatly broken up by agricultural settlements and fields. Nevertheless, the last northern remnants of the forest are located in Portuguese Guinea near one area of low sickling frequencies, and the other area in Eastern Liberia is in the center of the largest remaining block of tropical rain forest.

The frequencies of the sickle cell trait among the Pygmies also support this theory, although the comments of several authorities might seem to contra-

dict it. Regarding the Pygmies and Pygmoids, Hiernaux (1955:463) states; "They generally show a lower frequency of sicklemia than the surrounding populations, as shown in Table 2. In all cases but one, the frequency is lower in the Pygmoids. The most striking difference is between the Bondjo and Babinga, who are true Pygmies." Since most Pygmy groups have formed symbiotic relationships with their Negro neighbors, the frequencies among them can easily be explained by mixture, which is known to be occurring (Putnam 1948).

There is other evidence that *A. gambiae* has spread rather recently through the West African tropical rain forest. In the area around the Firestone Plantation in Liberia, shortly after the forest had been cut down, Barber, Rice, and Brown (1932) found that *A. gambiae* accounted for 46 percent of the mosquito population found in the native huts, while *A. funestus* accounted for 51 percent, and *A. nili* for 3 percent. However, at the present time in this same area, *A. gambiae* accounts for almost 100 percent of the mosquito population (Max J. Miller, personal communication). Barber, Rice, and Brown (1932) found holoendemic malaria, which is not present today; however, this change is due to malaria control and not to changes in the mosquito population. These figures thus indicate a significant increase in *A. gambiae* when the forest is cut down. Even more significant are Barber, Rice, and Brown's comments on the effects of reforestation on the mosquito population. They state (1933:629):

> We felt that it would be interesting to know what would be the condition of things when the rubber trees had grown and the unplanted ravines and swamps had become "rejunglized." We surveyed Mt. Barclay Plantation where the stream borders have grown up with brush or long grass. After a long search in the streams we found only two or three larvae, *A. mauritianius* and *A. obscurus*. In a pool near a village *A. costalis* was plentiful.

It can thus be seen that *A. gambiae* (the authors call the species *A. costalis*) was not present in natural water but only near a village. The authors also discuss "rejunglization" as a means of malaria control, but state that it would not be feasible due to the breeding places which would persist around the villages. In the absence of these villages, which are not built by hunting populations, and in the presence of unbroken tropical forest, the intensity of malaria would be much less. This seems to have been the situation in West Africa prior to the spread of slash and burn agriculture. Therefore, the spread of this agriculture is responsible for the spread of the selective advantage of the sickle cell gene, and hence for the spread of the gene itself.

SICKLE CELLS, DISEASE, AND HUMAN EVOLUTION

The preceding explanation of the distribution of the sickle cell gene and its relation to the culture history of West Africa has broad implications for the role of disease in human evolution. In considering the epidemiology of the sickle cell gene, Neel (1957:167) suggested that either the mutation which resulted in the sickle cell gene was very rare or else the spread of the gene was

at present favored by special circumstances of relatively recent origin. The detailed arguments of this paper would seem to show that there are indeed special circumstances of recent origin, while at the same time not excluding the possibility that the mutation is quite rare. The special circumstances are considered to be the conditions necessary to maintain holoendemic malaria due to *Plasmodium falciparum*. This parasite is in fact regarded as evolutionally the most recent species of malaria to parasitize man (Boyd 1949). If, as has been proposed, a mobile hunting population in the tropical rain forest could not develop holoendemic malaria, then this high endemicity would perhaps be even later than the adaptation of the parasite to man as its host. Since the agricultural revolution occurred only about 7000 years ago and spread much later to Africa, it appears that the development of the environmental conditions which are responsible for the spread of the sickle cell gene are relatively recent, as Neel postulated they should be.

The agricultural revolution has always been considered an important event in man's cultural evolution, but it also seems to have been an important event in man's biological evolution. Prior to this revolution, the size of the human population was controlled to a large extent by the size of its food supply, and man's ecological niche was comparable to that of the large carnivores, or more closely perhaps to that of a large omnivore such as the bear. With the advent of the agricultural revolution, the food supply was no longer the major factor controlling the size of human populations. Man broke out of his ecological confinement and there was a tremendous increase in the size of the human population, an increase which was limited only by the available land. Haldane (1949, 1956) has stated that disease became the major factor controlling the size of human populations at this time, and his statement seems to be supported in one case by the spread of holoendemic malaria.

Two results of the agricultural revolution seem to account for this change in the role of disease in human evolution: (1) the great changes in the environment, and (2) the huge increase in the human population. Both of these seem to be involved in the development of holoendemic malaria. First, when man disrupts the vegetation of any area, he severely disrupts the fauna and often causes the extinction of many mammals, particularly the larger ones. When this happens, there are many known instances of the parasites of these animals adapting to man as the new host (Heisch 1956). It is thus possible that the parasitization of man by *P. falciparum* is due to man's blundering on the scene and causing the extinction of the original host. Second, concomitant with the huge increase in the human population, this population became more sedentary and man also became the most widespread large animal. Thus, he became the most available blood meal for mosquitoes and the most available host for parasites. This change resulted in the adaptation of several species of the Anopheline mosquito to human habitations and the adaptation of many parasites to man as their host. Under these conditions, holoendemic malaria and probably many other diseases developed and became important factors

determining human evolution. It should be noted, however, that through domestication man has created large populations of other animals and these have influenced the epidemiology of several human diseases including malaria (for malaria examples, see Hackett 1949; Draper and Smith 1957). The sickle cell gene thus seems to be an evolutionary response to this changed disease environment. Hence, this gene is the first known genetic response to a very important event in man's evolution when disease became a major factor determining the direction of that evolution.

NOTE

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