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Evolutionary Response to Human Infectious Diseases

George J. Armelagos and John R. Dewey

The study of the evolution of man seldom takes into consideration the role of disease in this development. This is understandable since the evidence available is essentially inferential and consequently open to interpretation. These inferences are based on the actual paleontological record with additional information provided by the historical accounts of disease. We are also able to speculate on the occurrence of disease in prehistoric populations from the disease patterns in contemporary Homo sapiens and nonhominid populations. This study is an attempt to discuss infectious diseases in human evolution.

There are three variables which we must consider in the study of infectious diseases—the host, the pathogen, and the environment (Cockburn, 1963). The study of diseases in man, then, would involve the interrelationship of these variables. Although there have been changes in the host (in this case, man) and the pathogen, some of the most significant changes are those in the environment (Armelagos, 1967). It is important to note that the environment of man includes not only biotic, climatic, geologic, and geographic elements, but also all aspects of his culture (Bates, 1953). This presents somewhat of a dilemma, since man has used culture as his major mode of adaptation in an attempt to control the other aspects of his environment. The study of man’s culture—his technology, social system, and even his ideology—must be considered if we are to understand the disease patterns of man.

The role of culture is so significant in understanding the disease process that May (1960) has constructed a model in which culture is dealt with as a separate factor, as are the environment (which includes the pathogen) and the host. May illustrates the role of culture with particular disease patterns in North Vietnam. North Vietnam has two relevant geomorphological features: fertile delta and the fertile hills. Although rice is grown in the hills, the major area of rice cultivation is in the delta. The rice growers in the delta build houses on the ground, with a stable on one side and a kitchen on the other. The hill people, on the other hand, build houses on stilts with living rooms about 8 to 10 ft above the ground. The animals are kept underneath the houses, while the cooking is done in the living room.

The vector for malaria, Anopheles minimus, occurs in the hills, but the flight ceiling of this vector is about 8 or 9 ft and, consequently, the Anopheles encounter only the animals under the house. If the vector were to stray to the living room, fumes from the cooking would tend to drive it away. The malaria vector does not occur in the delta.

Some people have been forced to move to the hills under pressure of overpopulation in the delta. Typically, movement of the delta people to the hills has not resulted in the acceptance of the culture of the hill people. The delta tribes still build their houses on the ground, with the animals kept in the stables on the side. Food is cooked outside and brought into the house to be eaten in the smoke-free living room. This results in the Anopheles minimus feeding on the humans, whom they prefer to the nonhuman animals. This transfer results in the transmission of malaria to the new inhabitants. According to May, the people of the delta have been discouraged from relocating, feeling that the evil spirits in the hills do not like them. The intimate relationship between disease and culture noted by May is not unique; others (Hackett, 1937; Livingstone, 1958; Lambrechts, 1964; Alland, 1967; and Hudson, 1965) have presented similar interactions.

The Cultural Adaptation

The beginning of the cultural adaptation began about 2 million years ago with the emergence of man. During the Paleolithic, which lasted for 99% of human history, man was essentially a hunter and gatherer. Cultural development was excruciatingly slow. Pebble tools of the Oldowan culture persisted over a million years. The more refined hand axes and flake tools of the Abbevillian and Acheulean periods lasted another half-million years. There were other changes during the Lower Paleolithic which are relevant. The Australopithecines, the original hominids, were restricted to the tropical grasslands and exploited only a small portion of the available habitat. Although the diet of the Australopithecines, according to Howell (1964), consisted of a small amount of meat from fish, amphibians, reptiles, small mammals, and moderate-sized herbivorous ungulates, the major proportion was made up of gathered vegetal material.

During the latter part of the Lower Paleolithic, a period in which the hominids reached the Homo erectus stage of development, there was an increase in hunting ability. There are archeological sites which indicate preferential hunting. Seventy per cent of a large sample of bones found at Choukoutien, near Peking, China, belong to two species of deer (Howell, 1964). It is from this same site that the first evidence of fire is found. The major consequence of the cultural adaptation was an expansion of populations into the temperate zone. It is important to note that in our model we emphasize an expansion, rather than a migration, of population.

The changes during the latter part of the Lower Paleolithic, the Middle Paleolithic (130,000-40,000 B.P.), and Upper Paleolithic (40,000-12,000 B.P.) were variations of the same theme. The adaptation

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This is the fourth paper in the symposium "Pleistocene Man—Environmental Relationships."

March 1, 1970
of intensive hunting persists, with specialization in the Upper Paleolithic to differing environments. Again expansion is noted, this time into the tundra zone. It is during this period that we have the arrival of the first hominids into the New World (Griffin, 1964).

The close of the Pleistocene was marked by significant climatic changes in both the Old and New Worlds. The disappearance of the last glacier and a general warming trend caused significant changes in the distribution of large animals. Added to the apparent migration, the efficiency of Upper Paleolithic hunters led to the disappearance of many of the large animals in many areas. The hunting continued, but fishing and collecting became more important. Regional specialization continued in this period, the Mesolithic (12,800-8,000 B.P.).

In the Near East, these changes were responsible for an increased dependence on wild cereal which eventually led to semi-sedentary adaptation. This increased sedentarism, diversification of food sources, and decreased dependency on large animals were prerequisite to the domestication of plants and animals (Adams, 1964).

Although Neolithic development in the New World and Old World were independent, the consequences were similar. Sedentary villages were built to protect and care for the fields. There was a substantial increase in the size of residential units and total population. Increased food supply and the economic importance of children were causal factors for these increases. The agricultural adaptation led quickly to the development of sedentary villages in the Near East (4200 B.C.), urban centers (3100 B.C.), and preindustrial cities, and industrial cities (1800 A.D.).

Neolithic development resulted in drastic shifts in the ecological balance. Prior to the Neolithic, man had little observable effect on the environment (Sears, 1956). The utilization of fire (Stewart, 1956) represents one cultural practice which could have altered the landscape. In addition, the improvement of hunting techniques late in the Lower Paleolithic may have led to the extinction of the megafauna (Martin, 1967).

The adaptation we have been talking about is better reflected in population figures computed by Deevey (1960). By the end of the Lower Paleolithic, total population was 125,000 with a density of 0.00425/km². This increased to 1,000,000 (density 0.012/km²) in the Middle Paleolithic and to 5,320,000 (0.04 people/km²) in the Mesolithic. Following the Neolithic Revolution, there was nearly a sixteenfold increase over the Mesolithic population to 86,500,000 (1.4 people/km²). The increase in population, it is sad to say, continues.

Another factor which is relevant is the size of the social unit. A group of hunters and gatherers is not likely to increase much over 100 people and a more likely figure is 50-75 before fission occurs. The early agricultural villages at Jarmo, which were quite small, had over 150 people. Other agricultural villages would likely have had 300 or 400 people, but urban centers which followed far outshaded this. Ur, according to Woolley (1965), had a population of 350,000, while Sjoberg (1965) estimates a population of 100,000 people for the Valley of Mexico. By 1600 A.D. only 1.6 of the total European population was living in centers of 100,000 or more people. By 1700 A.D. this increased to 1.9%, and by 1800 A.D., to 2.2%. Following the Industrial Revolution, in Great Britain alone 10% of the population was living in centers of over 100,000. By 1990, Davis (1965) estimates that half the world will be living in urban areas of this size or larger.

The changes in cultural adaptation, with the resulting increases in population size, population density, and changes in the ecological balance, altered the disease pattern of man. Polgar (1964) suggests five stages in the disease history of mankind: hunting and gathering, settled villages, preindustrial cities, industrial cities, and the present. Our discussion of infectious disease in human evolution will utilize Polgar’s description of these stages.

The Hunting and Gathering Stage

For almost 2 million years man has subsisted on the animals he could hunt and on the edible plants he could gather. As one would expect, populations adapted to a hunting and gathering subsistence are small and are distributed over a wide area. In addition to their low density, these groups would have led a seminomadic existence. Small population size and low density would restrict the types of infectious disease which would have plagued them. Contagious diseases, for example, would not have had a large enough population base to have an impact on the evolution of these populations. Polgar suggests that the hunters and gatherers would have been afflicted with two types of disease—those which had adapted to the prehominids and persisted to infest them after speciation of the hominids, and those (zoonoses) which did not have human hosts but were accidentally transmitted to man. Such parasites as the head and body louse (Pediculus humanus), pinworms, yaws, and malaria would fall into the first category. Cockburn (1967b) would add that most of the internal protozoa found in modern man and bacteria such as Salmonella typhi and staphylococci would have been present. It is interesting to note that Livingstone (1958) would argue against malarial infections in early man. The small population size and bipedalism indicating a savannah adaptation would preclude the presence of malaria.

The second type of disease is that which has adapted to another host and is transmitted to man accidentally by insect bite, wounds, or from consuming meat of the infected animal. Sleeping sickness, scrub typhus, relapsing fever, tetanus, trichinosis, tularemia, leptospirosis, and schistosomiasis are examples of diseases which, Polgar speculates, may have been transmitted accidentally to man.

The range of the hunters and gatherers is a limiting factor for the kinds of parasites which would have been present. During the earlier period of the hunting and gathering stage, the hominids were restricted to the tropical zone. With an expansion of hominids into the temperate zone (by the time of Homo erectus), new and different parasites would have been present. It is important to note that by this time some food was being cooked, a process which would kill some of the parasites present.

Missing from the list of diseases which would have involved man prior to the Neolithic are contagious community diseases such as measles, influenza, smallpox, and mumps (Polgar, 1964). Burnet (1962) goes further and suggests that few viruses would have infected early man. Cockburn (1967a) disagrees strongly, since there are a number of viral infections found in monkeys. Although it is possible that monkeys studied may have contracted the viruses in captivity, the differences in the form of these viruses, according to Cockburn, are enough to argue against this.

The Settled Village Stage

The semi-sedentary encampments of the Mesolithic and sedentary villages of the Neolithic resulted in the concentration of populations in relatively small areas. As one could expect, this would
create new and different problems. In hunting and gathering societies, the disposal of human excrement presents no great problem since nomadic travel would preclude the accumulation of human waste (Heinz, 1961). It should be pointed out that in some cases, hunters and gatherers living in caves were forced to abandon them as the debris accumulated.

The sedentarism which is characteristic of the Mesolithic and Neolithic would provide new breeding places for many forms of life which harbor disease. In addition, domestication would have led to the herding of animals near the areas of habitation. Prior to this time, the dog was the only domesticated animal. Salmonella and Ascaris are carried by domesticated animals such as pigs, sheep, cattle, and fowl. C. A. Hoare (1957) has suggested that the trypanosomes were spread beyond the range of the normal host by domesticated animals. Polgar (1964) also suggests that the products of domesticated animals (milk, skin, hair) and the dust raised by the animals provide for the transmission of anthrax, Q Fever, brucellosis, and tuberculosis.

The expansion of agricultural societies into new environments created other problems. Audy (1961) has demonstrated that as new ground is broken for cultivation, scrub typhus increases. In this case, the agriculturists exposed themselves to the bites of insects as they toiled in the fields. Livingstone (1958) has impressively illustrated the relationship between the spread of agriculture, malaria, and sickle cell anemia. As the West African agriculturists expanded into the forest and destroyed the trees in the preparation of ground for cultivation, they encroached on the environment of the pongids. The pongids, which were the primary host of the Plasmodium falciparum carried by Anopheles gambiae, were exterminated or forced further into the forest. The mosquitoes quickly transferred to the hominids for their meals. Livingstone points out that agricultural activity, which provides new breeding areas for mosquitoes and provides a large population for the mosquitoes to feed, led to malaria becoming an endemic disease. Populations in this area have developed a genetic polymorphism—sickle cell trait—which gives those individual heterozygotes for the trait immunity to malaria. In other words, as the agriculturists expanded, malaria would increase. In response to the increase in malaria, the frequency of the abnormal sickle cell hemoglobin would increase.

### Preindustrial Cities

The expansion of the population which began in the Neolithic continued with the development of large urban centers in the preindustrial cities. The problem which faced the settled communities of the Neolithic are present but are significantly more difficult to control. The concentration of a large population in a small area creates problems in supplying food and water and removing human waste. Since many cities dispose of waste via their water supply, serious health hazards developed. Cholera, for example, was transmitted by polluted water. Even with our advanced technology, pollution is still a serious concern.

The increased frequency of contact between members of the population resulted in the transmission of disease by contact. Typhus was transmitted by lice which moved from person to person. Plague bacillus which was originally spread by rodents could, with the high population density, be transmitted by inhalation. During the preindustrial stage, viral diseases such as measles, mumps, chickenpox, and smallpox were also transmitted by contact.

Social change resulting from urbanization was responsible for alteration in the expression of some of the diseases. Prior to urbanization, syphilis was a nonvenereal disease, but with the changes in family structure, crowding, and sexual promiscuity, syphilis became a venereal disease (Hudson, 1965).

It was during this period that exploration resulted in the introduction of disease into new areas.

**Population during this period approached a size for the maintenance of diseases in an endemic form.** Cockburn (1967b) has suggested that a population of about one million is necessary for measles to be maintained as an endemic disease.

### Industrial Cities

Increase in population size and density was again a consequence of the cultural advances of the industrial revolution. The social and environmental changes were important. Industrial wastes increased pollution of water and air. UNSANITARY conditions in the slums were ideal focal points for the spread of infectious diseases, and imperialistic expansion transported disease into new areas.

Epidemics also created havoc in the industrial populations. Typhus, typhoid, smallpox, diphtheria, measles, malaria, and yellow fever epidemics are well documented for the late 18th and early 19th centuries (Polgar, 1964). Tuberculosis and respiratory diseases such as pneumonia and bronchitis were enhanced by the crowding and harsh working conditions. Perhaps the saddest consequence of the industrial period was the spread of epidemic diseases to populations which had not developed an immunity to them. Although contact had occurred earlier, in the preindustrial period, the impact was greater during the industrial period.

### Present

The advances that have been made in recent times have been quite remarkable; our understanding of the relevant features of infectious diseases has allowed us to make significant strides in preventing and controlling some infectious diseases. Even with these advances, infectious diseases are still prevalent in many areas. Attempts to control disease are more difficult with rapid transportation. Infectious diseases may be transmitted in hours to populations which, 50 years ago, were 2 weeks distant.

### The Evolutionary Response

The study of infectious diseases and their impact on human development is the host and the parasite (Motulsky, 1960). The duration of a human generation is much longer than that of the parasites which feed on man. This would favor evolutionary changes in the parasites leading to less severe manifestations of the disease. This is understandable since a parasite which causes the death of the host can then die from lack of a host.

The responses in the host were also significant. Haldane (1949) suggests that infectious diseases have been the most important selective factor in human evolution. Since the factors (i.e., large, dense population) which led to epidemic infectious diseases arose rapidly following the Neolithic revolution, the genetic factors would not have been present to provide immunity against these infectious diseases. In other words, the genotypes that were selected during the hunting and gathering stage would have provided little protection against the infectious diseases, but the genetic heterogeneity of the population would have been adequate to protect some individuals from the diseases. Lederberg (1963) disagrees, since many of the diseases which have animal reservoirs would be important in an epi-
demic sense. Instead of rapid selection acting on a large population, Lederberg suggests that the persistent application of small differentials over a long period of time, as characteristic of “reservoir disease,” could have developed factors of genetic immunity.

Motulsky (1963) states that there are three areas of concern in disease-susceptibility and resistance: (1) factors of immunity in the conventional antigen-antibody reaction; (2) generalized host factors; and (3) highly specific gene-determined factors which provide resistance.

Motulsky points out that there may be a genetic potential for antibody production, but it would be difficult to demonstrate in man. Lederberg (1959) has provided other data which would suggest a possible genetic variation in the response to antibody protection. Although not much is known about the inheritance of the nonspecific host factors in the response to infectious disease, they do appear to have a genetic basis. Efficiency of phagocytosis, levels of complements, antimicrobial factors in tissue, and serum inhibitors of microbial growth may have been important in providing immunity to diseases (Motulsky, 1963).

The highly specific genetic factors may have had a key role in the evolutionary response to infectious diseases. Although it would be impossible to demonstrate the genetic factors involved, populations appear to have developed a genetic immunity to disease. Motulsky (1960) states that when tuberculosis strikes a population which was not previously exposed to the disease, the mortality is high and the infection is acute. The individuals which are most susceptible to the disease would perish, while those with genetic characteristics which provide some resistance would survive. In subsequent episodes, the mortality is lower and infection is less severe. The differential susceptibility in different populations could result from a genetic difference. For example, American Indians and Eskimos developed a more acute tubercular infection. The evidence for genetic immunity is suggestive, however, since environmental differences in nutrition and sanitation may explain some of the population differences.

The evidence for highly specific genetic factors is more convincing in the metabolic polymorphisms which have evolved in response to disease (Motulsky, 1960). For example, the sickle cell trait, which provides resistance to malaria, has been discussed. Other polymorphisms have evolved in areas where malaria is endemic. The hemoglobinopathy thalassemia and glucose-6-phosphate dehydrogenase deficiency also appear to provide protection against malaria (Motulsky, 1963).

The evolution of genetic protection against infectious disease would have been essential for the survival of population, since epidemic diseases could destroy large segments of the population. In some instances, infectious diseases may act as a factor inhibiting population growth. In those populations in which epidemic diseases are still an important factor, increases in population are evidence. Cultural practices tend to maintain population size. As cultural groups are better able to prevent and control infectious diseases, the population increases at an alarming rate. In order to combat this increase in population, Polgar (1964) suggests that public health programs which are designed to control and prevent infectious diseases in countries with high fertility rates should include programs to limit population increase.

In addition to the problem of the exploding population, the control of infectious diseases has helped to increase life expectancy. The increase in longevity would have created new problems for the older segments of the population; increase in degenerative disease would have been a consequence. In a population in which the oldest individuals live to 60 years of age, degenerative diseases are relatively unimportant. Neel (1958) states that in the state of Michigan, of the deaths in 1953 from arteriosclerotic, hypertensive, or degenerative heart disease (which constituted 33.1% of all deaths), 7.4% occurred prior to age 50. By the 60th year, approximately 25% have died of degenerative heart disease. The remaining 75% of deaths due to degenerative heart disease occur after 60 years of age.

Recently, we were able to demonstrate that osteoporosis (loss of bone mass with age) occurs earlier and is more severe in prehistoric Nubian populations which compared to bone loss in a modern population. In the prehistoric Nubian population, the frequency of fractures due to severe bone loss was not evident. An examination of the mortality pattern would indicate why this should be the case. Approximately 40% of the population die before their 40th year. Only 15% live past 40 years and all are dead before age 60. In the United States, 91% live past their 40th year, 75% past their 60th, 29% past their 80th, and 6% past their 90th year. Since many individuals live past age 60 and osteoporosis continues, the decrease in bone mass becomes great enough to predispose the neck of the femur to pathological fracture. It should be pointed out that since these degenerative conditions occur in that segment of the population which is past reproductive age, selective responses to degenerative conditions could not occur.

With the possibility that we may be able to control infectious diseases in some populations, concern with degenerative conditions (Spiegelman, 1956) and population control should be two areas of future research.

Acknowledgment

Partial support was received from a grant (H. D. AM02771-01) from the National Institute of Child Health and Human Development, United States Public Health Service.

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BioScience Vol. 20 No. 5


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