REVIEW

MALARIA IN PREHISTORIC SOUTHEASTERN ASIA

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Abstract. This paper reviews the evolutionary and natural history of malarias; it is proposed that all human malarial parasites originated from zoonotic simian plasmodiids in tropical forests of southeastern Asia, during the terminal Pleistocene or early Holocene. The modes of malarial transmission among prehistoric natives of that geographic area is reconstructed, based primarily on ecological, archeological and ethnographic evidence.

Early Holocene hunters and food gatherers of southeastern Asia shared the same forest habitats as several mosquito members in the *Anopheles leucosphyrus* group, known to be efficient malarial vectors. These forest dwellers could have maintained endemic malaria, however at low levels due to their low population density. With the abundance and interactive roles in transmitting human malaria of the *An. dirus* and *An. minimus* mosquitos in forest fringe areas, the middle Holocene settled farmers occupying such habitats would have been subject all year round to highly endemic malaria. Generally much lower and less uniform transmission of the disease could have been found among early coastal occupants, in the presence of the less efficient *An. sundaicus* vector. Malaria was practically absent on lowland floodplains, extensively occupied by human populations since the first millennium BC onwards, due to lack of major vectors.

INTRODUCTION

Malaria has undoubtedly been one of the most crucial infectious diseases in the history of human-kind. It has been a prime cause of morbidity and mortality, and a strong selective agent in human evolution (Livingstone 1971, 1976). There is evidence that the disease had been highly endemic in many civilizations in the tropical and sub-tropical Old World since prehistoric times, probably associated with modifications of the natural environment by man (Livingstone 1958; Bruce-Chwatt 1965, 1988). Even as late as the mid twentieth century, some 250 million malaria cases still occurred annually world-wide, and about 2.5 million people died of this disease every year (Bruce-Chwatt 1987).

This paper attempts to resolve problems on the origin and spread of malaria in human populations. The natural and evolutionary history of the parasites will be investigated in the context of southeastern Asia, suspected as their ancestral home. Modes of disease transmission associated with diverse prehistoric human habitats are reconstructed for that geographic area.

CLIMATIC AND ENVIRONMENTAL BACK-GROUNDS OF SOUTHEASTERN ASIA

There is evidence that the late Quaternary glacial periods of high latitude corresponded to a drier, more seasonal climate in tropical Asia (Verstappen 1974, 1980). Studies of oxygen isotope determination from deep sea cores indicate that there would have been at least seven full glacial maxima during the past 700,000 years (Shackleton and Opdyke 1973; Shackleton 1982). Glacial-interglacial cycles were generally characterized by glacial periods of approximately 100,000 years, separated by shorter interglacial periods of about 10,000 to 30,000 years (Covey, 1984). During glacial periods, expansions of ice sheets in the Arctic and Antarctic took great quantities of water out of the hydrological cycle, substantially lowering world sea levels. For most of the Pleistocene, sea levels were approximately 30 to 80 meters below those at present; at the last glacial maximum (*ca* 18,000 BP), however, sea levels would probably have been as much as 130 to 150 meters below current levels, exposing Sundaland (including the present Sunda continental shelf, and the regions on or attached to it: Malaya, Sumatra, Java, Borneo, Palawan, and some other

small Islands) as a single land mass (Chappell and Thom, 1977). Expansion of land mass and deflection of ocean currents during the late Quaternary glacial maxima changed weather patterns and air circulation, thus causing a reduction in total annual rainfall by as much as 30% in southeastern Asia (Verstappen 1974, 1980). Mean temperatures near sea level in the tropics are thought to have been between 2°C (CLIMAP, 1976) and 5°C (Fairbridge, 1970; Verstappen, 1974; Rind and Peteet, 1985) lower than today.

Tropical forests in mainland southeastern Asia would have shrunk in extent with Pleistocene climatic aridity. In the archipelago, the two main cores of equatorial rain forest in western Malaysia and in New Guinea would have contracted, with a broader band of monsoonal forest and savanna between them (Steenis 1979; Verstappen, 1980; Whitmore 1984). Faunal remains from the Niah Caves, Sarawak, now located in the equatorial rain forest zone, indicate more open, drier environment during the late Pleistocene than during the early Holocene (Medway 1977). Steenis (1961, 1965) has suggested migrations of several drought plant species (*ie* teak - *Tectona grandis* Lf, sandalwood - *Santalum album* L, several Leguminosae and grasses) from an origin in mainland southeastern Asia into the archipelago with the extension of seasonal environment in the latter geographic area during glacial periods. Studies of alluvial and colluvial deposits corresponding to the last glacial period in Malaya indicate considerable erosion and valley filling, usually associated with savanna environment (Verstappen, 1974).

Shackleton (1977) has found, from curves of the variation in carbon-13 content in equatorial Pacific foraminifera, a marked increase in plant biomass and humus after 14,000 BP, suggesting the expansion of tropical rain forest with post-glacial climatic amelioration. Sea levels rose rapidly between 18,000 and 15,000 BP, oscillated at about 60 to 40 meters below present level for millennia, and then progressively increased to a level of about 10 meters below the present around 10,000 BP; rises in sea level carved Sundaland into Continent and Islands, doubling the length of shoreline (Dunn and Dunn, 1977). During the middle Holocene, around 5,000 BP, sea levels rose to almost 5 meters above current levels on all coasts of peninsular Malaysia, but then declined to the present level through a series of fluctuations of about 2 meters amplitude

and a period of 1,200 to 1,500 years (Tjia, 1987).

The Holocene climate and environment of southeastern Asia can be roughly inferred from rainfall patterns illustrated in Fig 1. The wettest climatic zone, where rain usually prevails all year round, lies within approximately 8° of the equator, including Malaya, Sumatra, western Java, Borneo, central Sulawesi and the eastern Philippines. These areas would have been covered almost entirely with tropical rain forest. At the center of the archipelago lies a north-south zone of monsoonal climate, extending from the northern Philippines to the Lesser Sunda Islands. Monsoonal climate prevails on mainland southeastern Asia north of Malaysia, comprising: Thailand, Myanmer, Lao PDR, Cambodia, Vietnam and parts of southern China. Forests in seasonal climatic zones tend to be more open, with a deciduous tendency, owing to the presence of a dry season and occasional severe droughts. Ever-green forests would have existed in areas where favorable moisture prevails, usually along water courses and foothills, as well as in mountainous areas.

THE EVOLUTION OF MALARIAL PARASITES

Mammalian malarias:

Mammalian malaria-parasites (Plasmodiidae) and their evolutionary precursors (Haemoproteidae) generally parasitize the same vertebrate hosts. Mammalian malarias are confined to Dermoptera (flying lemurs), artiodactyls, bats, rodents and primates; the last four orders, as well as elephant shrews, also harbor haemoproteids (Mattingly, 1983). The mammalian hosts of both parasite families are evolutionarily closely related. Gregory (1910) grouped Dermoptera, primates, bats and elephant shrews together in the common order, Archonta. Protangulatum, a primitive condylarth from the Cretaceous, due to striking similarities between its dentition and that of the earliest known fossil primate (Purgatorius), has been suggested to be ancestral to both the Palaeocene Hyopsodontidae-arboreal ancestors of the artiodactyls, and primates (McKenna, 1969, 1975; Simons, 1972; Mattingly, 1983). McKenna (1961, 1969) and Wood (1962) have noted the resemblances between the earliest fossil rodents (Paramyidae) and the earliest primates, while Simons (1972) grouped both the
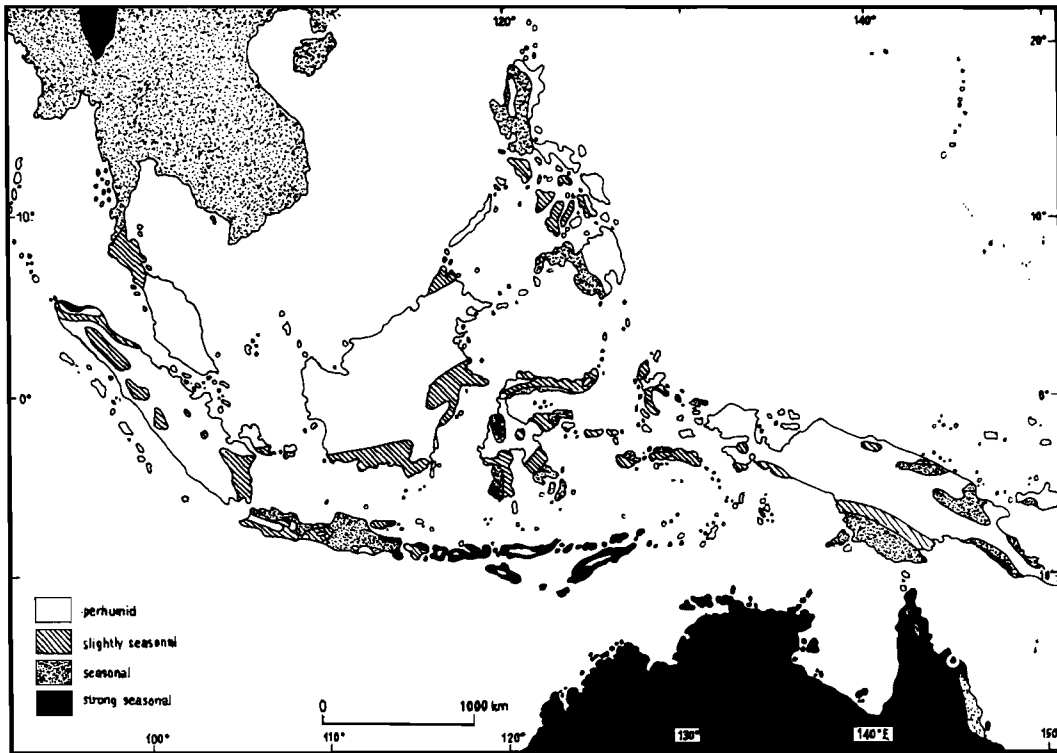
Fig 1–Rainfall Types of Southeastern Asia Based on Dry/Wet Period Ratios (Source: Whitmore, 1984).

rodents and Artiodactyla together with the primates. The common origin of mammalian Haemoproteidae, implied from the evolution of their hosts, has been suggested as the early Tertiary (Mattingly, 1983).

There is a general consensus among workers in the field that the genus *Plasmodium* was convergently reached (from haemoproteid ancestors) in different mammalian host orders and families (Ganham, 1966; Landau *et al*, 1976; Mattingly, 1983). Hosts of mammalian malarias, except for the Artiodactyla and elephant shrews, are almost exclusively forest animals. However, the artiodactyls have Paleocene arboreal ancestors, and Rhynchocyon, the most primitive elephant shrew genus, is a forest dweller (Butler, 1978). Based on the ecology of their primitive hosts, it is probable that most of mammalian plasmodiids originated in tropical forests. Some of the parasite species, particularly those parasitizing artiodactyls and elephant shrews, however, could have radiated with their hosts from the forest into a variety of more open habitats.

Malarias of non-human primates

All primate haemoproteids belong to the genus Hepatocystis (Garnham, 1966). They are confined to African and Asiatic monkeys and Asiatic apes. The presence of Hepatocystis in both cercopithecines and colobines in Asia has led Mattingly (1983) to conclude that the primate Hepatocystis or a more primitive haemoproteid ancestor had existed in Africa before the divergence between these two primate subfamilies during the middle Miocene. The parasite probably reached Asia with the hosts in the late Miocene.

African monkeys harbor only one malarial parasite, *Plasmodium gonderi,* found in mangabeys (*Cercocebus* spp), long-tailed green monkey (*Cercopithecus sabaeus*), and the drill (*Mandrillus leucophaeus*) (Coatney *et al,* 1971). The geographic range of this parasite in Africa is limited to the Upper Guinean forest and the area embracing southern Cameroon and Gabon, both forming forest refuges during pleistocene desiccations

(Eyles, 1963; Mattingly, 1983). Three *Plasmodium* species are currently recognized in African apes, *P. reichenowi, P. schwetzi* and *P. malariae* in lowland gorillas and chimpanzees (Collins and Aikawa, 1977). *Plasmodium reichenowi* and *P. schwetzi* are almost indistinguishable in terms of their morphology and life-cycle from *P. falciparum* and *P. vivax* in man, respectively (Coatney *et al*, 1971). Man and African apes are thought to share *P. malariae* (Bray, 1963). The main areas of distribution of the plasmodiids of African apes include the forest refuges mentioned for those of *P. gonderi,* as well as the forest of the Congo Basin (Mattingly, 1983).

In contrast to African monkeys, Asiatic anthropoids harbor numerous plasmodiid species. *Plasmodium inui, P. cynomolgi* and *P. knowlesi,* found in macaques and langurs, are widely distributed in southern and southeastern Asia (Eyles, 1963). *Plasmodium fieldi, P. coatneyi* and *P. youngi* are restricted to western Malaysia, *P. fragile* to India and Sri Lanka, and *P. simiovale* to Sri Lanka only (Eyles, 1963; Collins and Aikawa, 1977); all are found in macaques. Five species are currently known for gibbon plasmodiids: *P. hylobatei* (from the southeastern Asian mainland, Java and Sarawak), *P. eylesi, P. jefferyi, P. youngi* and one unnamed species (all the last four species are from western Malaysia) (Collins and Aikawa, 1977). *Plasmodium pitheci* and *P. sylvaticum* are the two plasmodiid species of the Borneo orang-utan (Peters *et al*, 1976; Mattingly, 1983).

Among New World monkeys, there are two plasmodiid species. *Plasmodium simium* is found in howler (*Alouatta* spp) and woolly spider (*Brachyteles arachnoides*) monkeys, and *P. brasilianum* is found in a wide range of primate hosts (Coatney *et al*, 1971). The areas of high incidence for the former are confined to the coastal and some inland forests on southern Brazil (Coatney *et al*, 1971). The latter parasite species is widely distributed in Panama, Colombia, Peru, Venezuela and northwestern Brazil (Collins and Aikawa 1977; Mattingly, 1983). There are large areas, however, with appropriate host animals, where the parasites are not found, or where infections in the same monkey genera vary considerably (Coatney *et al*, 1971). *Plasmodium brasilianum* and *P. simium* are almost identical, morphologically and biologically, to *P. malariae* and *P. vivax* in man, respectively. Most workers agree, on bases of the

parasite distribution and similarities with those malarias of humans, that both were acquired by New World monkeys from human hosts (as anthroponoses) in post-Columbian times, and that there would have been neither human nor non-human primate malarias in the New World before European contact (Dunn, 1965; Coatney *et al*, 1971).

The present opinion among most workers on the evolution of primate plasmodiids is that the quartan group of parasites (*P. inui, P. brasilianum* and *P. malariae*) is the most ancestral, followed by the tertian group (comprising the ovale sub-group: *P. fieldi, P. simiovale* and *P. ovale,* and the vivax sub-group: *P. vivax, P. gonderi, P. hylobati, P. cynomolgi, P. cyclopsi, P. pitheci, P. youngi, P. simium, P. eylesi, P. jefferyi* and *P. schwetzi*), the quotidian *P. knowlesi,* and the most recent falciparum group (*P. falciparum, P. coatneyi, P. fragile* and *P. reichenowi*), respectively (Garnham, 1966; Bruce-Chwatt, 1965, 1988; Coatney *et al*, 1971; Mattingly, 1983).

Garnham (1966) has oriented the evolution of malarial parasites, relative to the general evolutionary trends of their primate hosts. He proposes the genus *Hepatocystis* and the ancestral quartan group of malarial parasites to have evolved with their lemuroid hosts in the Tertiary. During the oligocene, the Old World monkeys of superfamily Cercopithecoidea acquired, in the course of their evolution, benign tertian and quotidian parasites. It is proposed that it was in the lower Pleistocene, along with the evolution of Pongidae and Hominidae, that the subgenus *Laverania (P. falciparum* and *P. reichenowi*) evolved and became parasites of man and African apes. This point of view has also been supported by Bruce-Chwatt (1965, 1988), who made a strong attempt to show that most of the primate plasmodiids have an African origin, as did their hosts.

An alternative view, proposed by Coatney *et al* (1971), is that a hepatocystis-like ancestor evolved into the plasmodiid level after an ecological separation of Asian and African monkey groups. Most of the primate plasmodiids could have originated in forests of southern and southeastern Asia, where numerous species of plasmodiid parasites are currently found. The ancestral quartan plasmodiid parasites of southern and southeastern Asia could have given rise to contemporary quartan, tertian and quotidian species in various primates.

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Whether a tertian parasite, *P. gonderi,* evolved from an extinct quartan ancestor of Africa, or whether it originated from an ancestral parasite of Asia, remains equivocal. In the authors' opinion the hominids invading southeastern Asia from Africa, probably more than a million years ago, would have shared the same tropical forest environment as their non-human primate relatives, and most likely received plasmodiid parasites (the ancestors of *P. malariae* and possibly *P. vivax*) from them. Further parasite speciation took place in the African continent, from the Asiatic quartan or tertian stock introduced into Africa by hominid contacts from Asia, eventually resulting in *P. schwetzi, P. ovale* and *P. falciparum-reichenowi* complex (Coatney *et al,* 1971).

In Africa, *P. gonderi* fails to reoccupy forests of the Congo Basin, even to the limited extent achieved by the plasmodiids of African apes, and also fails to infect the readily susceptible baboons and guenons inhabiting the same geographic areas as its natural hosts (Mattingly, 1983). This phenomenon suggests that the unknown African mosquito vectors are not efficient in transmitting the malaria among non-human primates, due to their own limited geographic, ecological, and host ranges. Recent evidence provides support for an origin of New World monkeys from an African anthropoid stock in the early Oligocene (Ciochon and Chiarelli, 1980). If the immediate African origin of New World monkeys is valid, then the probable absence of plasmodiid parasites in ancestral New World monkeys hints that malarias were also rare or absent in their African simian ancestors. The relative paucity of malarial parasites and the lack of quartan species in African monkeys have made the possible Asian origin of most primate malarias more convincing.

The ecology of malarial transmission in southern and southeastern Asia favors the speciation of primate plasmodiids. All the known vectors of simian malaria in those geographic areas belong to the *Anopheles leucosphyrus* group of mosquitos. Members of this species group share common ecological niches of monsoonal and tropicalrain forests, with a tendency to be obligate primate feeders (Warren and Wharton, 1963). Several species are known to be susceptible to most simian plasmodiids (Collins and Aikawa, 1977; Collins, 1988). The geographic distribution of *An. leucosphyrus* mosquitos covers the known range of simian malaria, from southwestern India and Sri Lanka eastwards to Sulawesi, and north to southern China, Taiwan and the Philippines (Warren and Wharton, 1963). The wide range and abundance of these mosquitos would have facilitated the transmission of plasmodiids among different primate species. The preferential feeding developed by an anopheline vector on particular primate host species allowed adaptation of the parasites to specific alternate hosts, resulting in parasite speciation. Tropical forests of southeastern Asia provided numerous complex ecological niches to support considerable population densities of non-human primates, maintaining endemic malaria. For example, there are at least six sympatric higher primates in Malaysia that share the same forest habitat (Whitmore, 1984), with an average primate density at eight lowland evergreen forest sites of 13.5 groups per square kilometer (Marsh and Wilson, 1981; cited in Whitmore, 1984). From these ecological inferences, most of contemporary simian malarias could have evolved in southern and southeastern Asia, from Hepatocystis or probably a quartan plasmodiid ancestor, reaching tropical Asia with their anthropoid hosts from Africa in the Miocene.

Human malarias

There are four plasmodiid species harbored by man, *P. malariae, P. vivax, P. ovale,* and *P. falciparum.* Current opinion favors parasite origin in non-human primates of Africa or of southeastern Asia. The life cycles and general morphology of all human plasmodiids are very similar to the related parasites of non-human primates (Collins and Aikawa, 1977; Collins, 1988). *Plasmodium vivax* resembles, both morphologically and biologically, *P. cynomolgi* of the Asian macaques and langurs, and *P. schwetzi* of the African apes. *Plasmodium malariae* is identical in man and the African apes. *Plasmodium ovale* resembles *P. fieldi* and *P. simiovale* of the Asian monkeys. *Plasmodium falciparum* resembles *P. reichenowi* of the African apes. Except for its gametocyte morphology, *P. falciparum* also has many similarities with *P. fragile* and *P. coatneyi* of southern and southeastern Asian macaques, respectively.

There is a general consensus that *P. vivax* originated from *P. cynomolgi* of macaques (Contacos and Coatney 1963; Coatney *et al,* 1971; Livingstone, 1971). The latter parasite can be transmitted

effectively via the bites of infected mosquitos from monkey-to-man, man-to-man, and man-to-monkey (Chin *et al,* 1968; Coatney *et al,* 1971). The macaques had a wide geographic range in the past, extending westwards from southeastern Asia to India, the Middle East and Europe. The zoonotic *P. cynomolgi-vivax* complex could well have originated within a limited distribution of *An. leucosphyrus* mosquitos in southern and southeastern Asia, because the macaques living outside the geographic range of these vectors, such as those in northern-central India, are not known to harbor any malaria (Coatney, 1963).

Plasmodium malariae could have evolved from its closely related parasite, *P. inui,* of Asian macques and langurs. The latter parasite is a species complex with wide geographic and host ranges throughout most of southeastern Asia (Collins, 1988). *Plasmodium inui* can be transmitted to man via the bites of infected mosquitos (Coatney *et al,* 1966, 1971).

The distribution of *P. ovale* in human populations is sporadic. The parasite is most prevalent in western Africa, suggested by Coatney *et al* (1971) as its ancestral home. Outside Africa, *P. ovale* malaria is also readily endemic in the Philippines and New Guinea (Lysenko and Beljaev, 1969; Coatney *et al,* 1971), with sporadic indigenous cases reported from Thailand (Cadigan and Desowitz, 1969) and the Thailand-Myamar border area (Somboon and Sivasomboon, 1983). An African origin of *P. ovale* is questionable, however, because an ancestral form of the parasite is lacking among non-human primates of that continent. On the other hand, there are two plasmodiid species, parasitizing macaques of Sri Lanka and Malaysia, that resemble *P. ovale,* namely *P. simiovale* and *P. fieldi,* respectively (Eyles *et al,* 1962b; Dissanaike *et al,* 1965a). Therefore, the evolution of *P. ovale* from an immediate simian origin of southern or southeastern Asia is also plausible.

The prevalence of *P. vivax* probably accounts for the rarity of *P. ovale* malaria in tropical Asia. Both species are similar tertian parasites. They are probably complete ecological competitors, and cannot coexist in the same host populations (Livingtone, 1984). There is evidence that Duffy negative blood group (Fy°Fy°) confers solid protection against *P. vivax,* but not against any other human plasmodiid infections (Miller *et al,* 1976). The frequency of Duffy negative is extremely high in parts of western

Africa, where *P. ovale* is endemic. Livingstone (1984) has suggested that *P. ovale* probably well survives in western African populations, with high frequencies of Duffy negative causing preadaptation of human hosts to *P. vivax* infections. The rarity of *P. ovale* malaria in southern and southeastern Asia could be associated with low Duffy negative frequencies in natives (Mourant *et al,* 1976).

The origin of *P. falciparum* is somewhat equivocal. Several authors favor an African origin of the parasite, because its closely related congener, *P. reichenowi,* is found naturally infecting African apes (Bruce-Chwatt, 1965, 1988; Garnham, 1966; Coatney *et al,* 1971; Livingstone, 1971). It is equally possible that the African apes received the parasite from a human analog. An immediate ancestor of *P. falciparum* from the African simian stock has been competed by two falciparum-like parasites naturally infecting macaques of southeastern and southern Asia: *P. coatneyi* of Malaya and the Philippines (Eyles *et al,* 1962a, 1963), and *P. fragile* of southern India and Sri Lanka (Dissanaike *et al,* 1965b). Several attempts to infect man with these three falciparum-like parasites in the laboratory have been unsuccessful (Dissanaike *et al,* 1965b; Coatney *et al,* 1971; Garnham, 1965). *Plasmodium reichenowi* also fails to grow in *Macaca mulatta* (rhesus macaque), *Cercopithecus schmidti,* and *Cercocegus atys* (Coatney *et al,* 1971), and fails to infect several anopheline mosquitos, including universal experimental vectors from the *An. dirus* complex (Coatney *et al,* 1971). The specificity of *P. reichenowi* infections to only few natural (vertebrate and invertebrate) hosts may exclude the parasite from potential zoonosis. On the contrary, the Asian parasites, *P. coatneyi* and *P. fragile,* can be experimentally established in several monkey species other than their natural hosts, either by inoculations of parasitized blood or by sporozoites (Eyles *et al,* 1962a, 1963; Garnham, 1965). They can also readily infect and produce sporozoites in several members of the *An. leucosphyrus* group (Coatney *et al,* 1971), the Asian mosquito vectors transmitting malaria in both man and non-human primates. Therefore, evolution of *P. falciparum* in southern or southeastern Asia is more convincing than an African origin for the parasite, on ecological grounds.

McCutchan *et al* (1984) have reported that the deoxyguanosine + deoxycytidine (dG + dC) pattern of *P. falciparum* is more akin to those of the avian and rodent plasmodiids (*P. lophurae* and

P. berghei, respectively) than to other human and non-human primate malarial parasites (*P. vivax, P. knowlesi, P. fragile* and *P. cynomolgi*). These authors have proposed that *P. falciparum* is evolutionarily more closely related to avian and rodent parasites than to other human and non-human primate plasmodiids. Phylogenetic closeness between *P. falciparum* and *P. berghei* is questionable, however, owing to the marked difference between their genomic sizes. *Plasmodium falciparum* contains 3.8×10^8 base pairs with 10% repetitive sequences, whereas *P. berghei* contains 2×10^7 base pairs with repetitive sequence frequencies varying between 3% and 18% (Dore *et al,* 1980; Hough-Evans and Howard, 1982; Scheibel and Sherman, 1988).

A more recent phylogenetic analysis among the plasmodiid species, based on small-subunit ribosomal RNA gene sequences, accomplished by Waters *et al* (1991), has revealed a distant relationship between *P. falciparum* and *P. berghei,* while it supported a greater evolutionary closeness of the former with the avian (*P. gallinaceum* and *P. lophurae*) than with the other human (*P. vivax*) and non-human primate (*P. fragile*) malarial parasites. These authors suggest the origin of *P. falciparum* as a lateral transfer of the avian parasite to a human host. Differences between the parasite species, based on ribosomal RNA sequences expressed during the parasite asexual cycles in vertebrate hosts, however, could be equivocally attributed to genetic adaptation of the parasites to different vertebrate host species. Also, knowledge on zoonotic transmission of the avian parasite, necessarily required in support of that evolutionary hypothesis, is currently lacking.

THE ECOLOGY OF MALARIAL TRANSMISSION

Malaria is endemic in an area where there has been a constant measurable malarial incidence both of cases and of natural transmission over a succession of years (Pampana, 1969). The continuous transmission of malaria requires a proportion of the human population susceptible to parasitic infection, a sufficient gametocyte reservoir, and an adequate anthropophilic anopheline population to serve as the parasite's vector.

This section reviews the ecology of malarial transmission, in conjunction with archeological evidence, for prehistoric human habitats of southeastern Asia: inland tropical forests, forest fringes, coastal areas, and flood plains, respectively.

Inland tropical forests

Human ecology: *Homo sapiens sapiens* would have spread throughout southeastern Asia during the late Pleistocene. Modern man apparently reached the Australian Continent from the Sunda continental shelf, necessarily across a still substantial ocean gap, during low sea levels some 35,000 to 40,000 years ago (Kirk, 1981). Several archeological sites occupied by prehistoric human populations have been discovered both in archipelago and mainland southeastern Asia, dating between 40,000 and 12,000 BP (Bellwood, 1985, 1990; Ha Van Tan, 1977; Anderson, 1986). The majority of late Pleistocene hunters and food gatherers would presumably have been well adapted to drier environments, widespread in southeastern Asia at that time. Faunal remains and stone tools from several late Pleistocene archeological assemblages indicate that these people were capable of hunting large game animals in relatively open habitats (Medway, 1977; Bellwood, 1985). Although several of the late Pleistocene archeological sites are now located in the peripheral equatorial tropical forest zone (*ie* Niah Caves in Sarawak, Tabon Cave in Palawan, Tingkayu Valley and Madai-Baturong sites in eastern Sabah), the immediate environment of these sites would have been considerably drier, with more seasonal variation, during Pleistocene human occupations than at present (Bellwood, 1990). Archeological surveys in the deep equatorial rain forest of southern Malaya, eastern Sumatra, and Borneo, have failed to detect any trace of human occupation during the Pleistocene (Harrison, 1970; Hanbury-Tenison, 1980; Bellwood, 1990).

Since the beginning of the Holocene, dense tropical forests have proliferated extensively, both at the fringe of the equatorial tropical forest zone and in mainland southeastern Asia. Archeological evidence of human occupation within tropical forests is obvious in both areas. Game mammals tended to be smaller in size and lower in biomass per unit area in early Holocene forests than in the late Pleistocene, more open habitats (Pfeffer, 1974, cited in Bellwood, 1985). However, dense tropical forests provided complex resource arrays (*ie* diverse plant species, small game animals, and fresh water shellfish) to be exploited by early Holocene hunters and food gatherers.

There are numerous archeological sites on the mainland, dating from approximately 14,000 to 3,000 BP demonstrating common human exploitation of forest resources and a common tool tradition, named by Gorman (1970) as the Hoabinhian technocomplex. The name Hoabinhian has been derived from the Province of Hoabinh in upland northwestern Vietnam, where the typical stone tools were first recognized (Colani, 1927, cited in Higham, 1989). Inland Hoabinhian archeological sites are widely distributed in southeastern Asia, from Southern China to Malaysia, and from Vietnam to Greater Assam (Sharma, 1984; Higham, 1989). A typical occupation site is a rock-shelter near perennial stream(s), located on the karstic topography of the tropical forest interior (Gorman, 1970; Higham, 1989). An inland rock shelter was probably compatible with temporary occupation by groups of hunters or food gatherers, given to occasional movements (Anderson, 1989). Natural food resources exploited by these nomads included small to medium size mammals, reptiles, fresh water shellfish, edible fruits and plant parts available in surrounding environments. An analysis of an inland Hoabinhian economy can be found in Gorman (1970) for Spirit Cave, an archeological site in northwestern Thailand.

The archipelago populations of southeastern Asia demonstrate arrays of the forest adaptation similar to their contemporaneous continental counterparts during the early Holocene (ca 12,000 to 8,000 BP). Evidence comes from several archeological sites, Niah Caves in Sarawak, Madai and Agop Sarapad Caves in Eastern Sabah, Leang Burung 1 and Ulu Leang Caves on Sulawesi, and others occupied during that time period (Bellwood, 1985; Whitten et al, 1987). Faunal records from Niah Caves indicate a general decline in mammal size and local extinction of the Malayan tapir, attributed to the proliferation of dense forest during the early Holocene (Medway, 1977; Bellwood, 1985). Archeological assemblages at Niah Caves and Ulu Leang indicate exploitation of various animals (ie pigs, babirusa, primates, bats, rodents, snakes, lizards and land snails) and fresh-water shellfish, available in tropical forest interior, by prehistoric inhabitants (Bellwood, 1985; Whitten et al, 1987).

Malarial ecology: Several mosquito species of the *An. leucosphyrus* group in the Neomyzomyia series are the principal vectors of human malaria in

tropical forests of southeastern Asia. *Anopheles dirus* Peyton and Harrison, itself a complex of at least seven isomorphic species, is a primary vector of human malaria in monsoonal and evergreen forests on the mainland (Baimai, 1988). Its habitat does not expand far from the peripheral (in northern Malaya) into core regions of the equatorial tropical rain forest. Eyles *et al* (1964) reported from Cambodia that *An. dirus* preferentially fed on man, although it was readily attracted to monkeys in the monsoonal forest canopy. *Anopheles balabacensis balabacensis* Baisas is known from Palawan and Balabac Islands (of the Philippines), Sabah, Brunei, the extreme north of Sarawak, and western Java (Harbach *et al*, 1987). *Anopheles leucosphyrus* Donitz is a species complex consisting of at least two allopatric species, A and B; the former widely distributed in Peninsular Malaya, Sarawak and Kalimantan, and the latter probably confined to Sumatra (Baimai, 1988). The *Anopheles leucosphyrus* complex is incriminated as a vector of human plasmodiids in Sumatra and Sarawak (Colless, 1957; Baimai, 1988), as well as of monkey plasmodiids in Malaya (Wharton *et al*, 1962). The geographic distribution of these principal vectors of human malaria is shown in Fig 2.

All the known natural vectors of monkey plasmodiids in southern and southeastern Asia belong to the *An. leucosphyrus* group. *Anopheles hackeri* has been found naturally infected with *Plasmodium inui, P. knowlesi, P. coatneyi, P. fieldi* and *P. cynomologi, An. balabacensis introlatus* with *P. fieldi* and *P. cynomolgi, An. leucosphyrus* with *P. inui,* and *An. elegans* with *P. inui, P. cynomolgi* and *P. fragile* (Wharton *et al*, 1962; Wharton and Eyles, 1961; Warren *et al*, 1963; Collins and Aikawa, 1977). The first three vector species are known from the equatorial rain forest zone of Malaya, and the last is known from Sri Lanka.

Wharton *et al* (1964) reported that the Malayan mosquito vector of monkey plasmodiids, *An. hackeri,* had a definite preference for feeding on monkeys in the canopy. The other two vector species, *An. leucosphyrus* and *An. balabacensis introlatus,* while readily attracted to man on the ground, were rare, preferring to feed on monkeys. The authors then suggested that natural transmission of simian malarias to man would be more common in the monsoonal and evergreen forests on the mainland, where the *An. dirus* complex was abundant and intimate monkey-man contact via mosquitos was
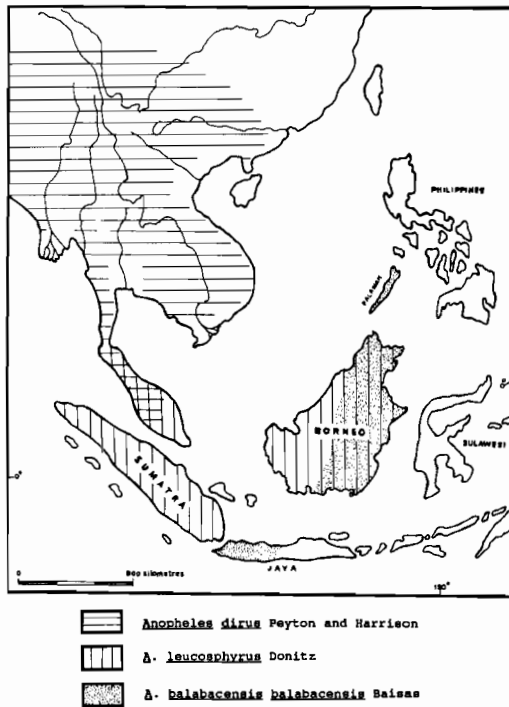
Fig 2–Distribution of the Principal Malarial Vectors in the *Anopheles leucosphyrus* group in Southeastern Asia (Sources: Harbach *et al*, 1987; Baimai 1988).
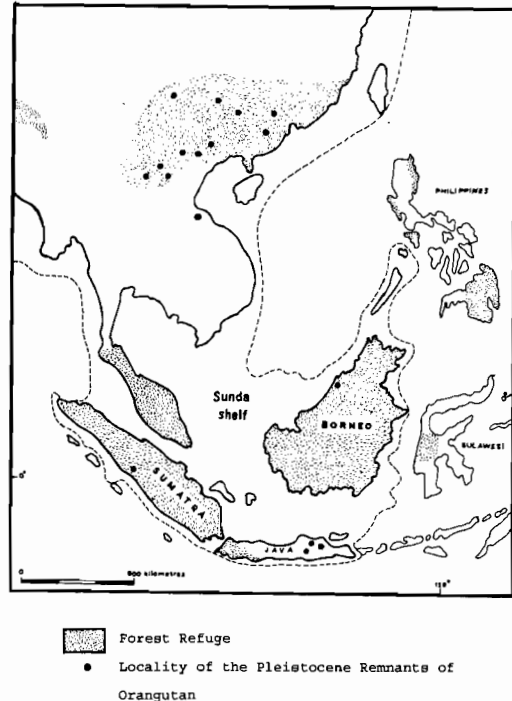

Fig 3–Pleistocene Forest Refuges in Lowland Southeastern Asia (Sources: Kahlke 1973; Meijer 1982).

substantial, than in the equatorial tropical rain forest of Malaya. It is worthy of note that the *An. dirus* complex has been proven to be susceptible to most primate plasmodiids (Collins, 1988); the sporozoite rates from naturally infected mosquitos are among the highest reported for Asia for any vector species (Eyles *et al*, 1964; Rosenberg and Maheswary, 1982).

At the Pleistocene glacial maxima, savanna and open woodland occupied much of what is now monsoonal and evergreen forest on the mainland. Rain forests were probably reduced to isolated refuges. Postulated forest refuges in lowland southeastern Asia during Pleistocene desiccations are illustrated in Fig 3. The distribution of Pleistocene remnants of the Orangutan (*Pongo* spp), well adapted to tropical rain forest, agrees mostly with that of forest refuges. Non-human primates and their plasmodiid mosquito vectors (of the *An. leucosphyrus* group) would have been confined within these forest refuges for most of the Pleistocene. Human forest adaptation was pronounced in

southeastern Asia subsequent to the last glacial maximum, *ca* 18,000 BP (Bellwood, 1985; Anderson, 1989). Early forest nomads came into close contact with non-human primates and probably acquired zoonotic malaria from them. The monkey-to-man transmission of malaria would be more common in monsoonal and dry evergreen forests of mainland southeastern Asia, with the presence of the *An. dirus* complex, than in the equatorial rain forest zone. The human parasites could have spread, and have become common in most of the tropical Old World during the middle Holocene. Malaria was evident in China, India, Mesopotamia, Greek, and Egypt, subsequent to the development of agriculture (Bruce-Chwatt, 1965, 1988). The disease endemicity outside tropical Asia was probably associated with high densities and sedentism of human populations, and with the adaptation of malarial vectors to man-made habitats, as investigated by Livingstone (1958, 1976) for western Africa.

One of the crucial problems with a deep anti-

quity of human malaria is whether a virulent parasite like *P. falciparum* could be maintained endemically among early nomadic forest dwellers of southeastern Asia, presumably with very low population densities. Studies on contemporary hunters and food gatherers of that geographic area, however, may provide some clues concerning disease transmission among their predecessors during the terminal Pleistocene and early Holocene.

Zulueta (1956) has reported that the Punan, a primitive hunting-gathering group of interior Sarawak, suffer from malaria, but with much lower spleen and parasite rates than neighboring settled farmers. There is evidence from the Negritos of interior Malaya that small bands of food gatherers move every few days within a limited territory, but habitat ranges among bands (particularly of the same tribe) overlapped considerably (Skeat and Blagden 1906; Carey 1976). Assuming that a small band of nomadic hunters harboring malaria stays in one particular place for a few days, the forest mosquito vectors within 1 to 3 kilometers from a temporary campsite, according to the flight ranges of major vectors from the *An. dirus* complex (Rosenberg, 1982), would have the opportunity to become infected with human parasites. It takes several more days for the mosquitos to become infective, during which the same hunting group may have already left the area. The infectivity period of vectors would last for a considerable length of time; Gould *et al* (1966) reported that a large proportion of adult female *An. dirus* captured alive from the field could survive for over 30 days longer, under laboratory conditions. Any hunting group that enters the domain of readily infective mosquitos, which may now cover an area of more than 3 kilometers in radius from the abandoned campsite, is at risk of becoming infected by malaria. The endemicity of malaria maintained among early nomadic hunters by this means would have been much lower than among settled villagers with higher population densities, in which a transmission cycle of the disease is completed within the same host populations.

The *An. dirus* complex has proven to be a group of efficient vectors for human malaria in southeastern Asia (McArthur, 1947; Scanlon and Sandhinand, 1965). It is exclusively a group of forest mosquitos that attack man readily only at forest fringes or within forest interior localities (Rosenberg and Maheswary, 1982). Eyles *et al* (1964) found during their study in Cambodia that the population of *An.*

dirus was eight times larger in deep monsoonal forest than near villages. The preferred breeding places for these mosquitos are small, stagnant, often turbid, transitory pools completely protected under the shade of forest canopy (Colless, 1957). Their breeding places can be destroyed completely with forest clearance. Rosenberg (1982) has found that the breeding habitats of *An. dirus* were confined to the seepage pools on the shaded banks of permanent streams during the dry season. They expanded prolifically to temporary pools on the forest floor during the wet season. In the latter breeding habitat, gravid females usually deposit eggs on moist soil above the water level, resulting in a synchronous hatching of the eggs, following a single heavy rainfall. Adult female *An. dirus* form a mass flight seeking blood meals, within a considerable flight range, mentioned earlier (Rosenberg, 1982). These breeding and feeding behaviors imply that a large number of female *An. dirus* could become synchronously infected with the plasmodiid parasites, and later on, infective for malaria to humans. A large number of infective females in a single mosquito cohort would be able to transmit malaria thoroughly in any nomadic group that opportunistically come into contact with them, thus providing a mechanism for maintaining malaria endemically among early Holocene hunters and food gatherers, with low density and sparsely distributed populations.

Forest fringe

Human ecology: A profound change in the relationships of Holocene inland dwellers of southeastern Asia to their environment came with the development of agriculture and a sedentary life style in the fourth millennium BC. Early agricultural villages are evident archeologically in several parts on the mainland: northeastern Thailand (the Khorat Plateau), the eastern and western upland borders of central Thailand, central Cambodia, and upland northwestern Vietnam. The distribution of archeological sites in these areas is illustrated in Fig 4.

Early village economy was primarily based on rice cultivation, stock raising, and hunting-gathering. Early villages from the fourth to second millennia BC shared a common environment. They were usually located at forest fringes, on low terrace soils of old river basins in the vicinity of a confluence of small, permanent streams (Wichakana, 1984;
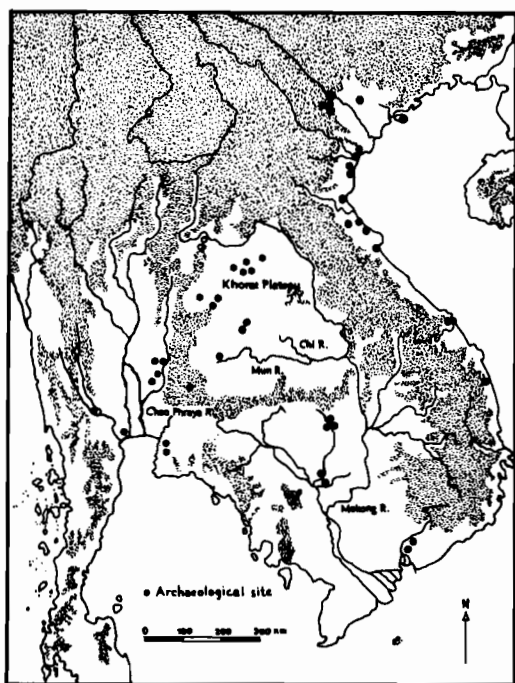
Fig 4–Distribution of Middle Holocene Coastal and Inland Sedentary Villages on the Southeastern Asian Mainland (Source: Higham 1989).

Fig 5–Distribution of Archaeological Sites Associated with Landforms and Streams in the Songkhram Valley, Northeastern Thailand (Source: Wichakana 1984).

Higham, 1989). The climate was monsoonal, with a marked dry season. Such localities were prone to mild seasonal-flooding, suitable as a natural habitat for rice (White, 1984). The dependence on suitable land for rice cultivation in a relatively open habitat and the higher population density supported by food production would have set the ecology of early farmers apart from that of earlier inland nomads and of coastal occupants.

Studies on micro paleo-environments for early agricultural villages have been conducted for sites in northeastern Thailand (Higham, 1975; Higham and Kijngam, 1982). Since almost all early inland villages on the southeastern Asian mainland were located in geographically (as well as climatically) comparable areas, the settlements in northeastern Thailand may serve as a representative example.

The earliest phase of sedentary human occupation in northeastern Thailand started in the fourth millennium BC, in the upper part of the Sakon Nakhon Basin. The distribution of archeological sites, in association with land forms and streams in this area, is illustrated in Fig 5. The occupation
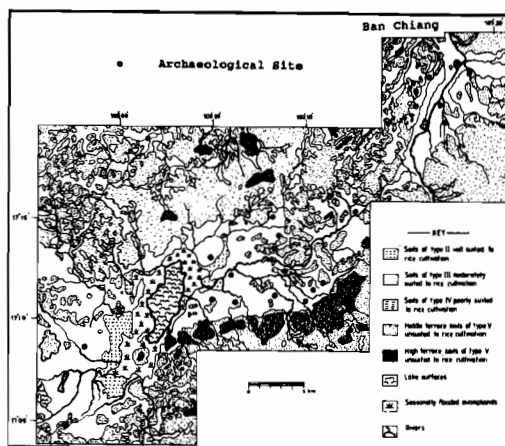
sites were usually located on slightly elevated ground, adjacent to tracts of low terrace soil and a confluence of tributary streams; most of the middle and high terrace areas immediate to the sites would have been forested during early occupations. Monsoonal climate and terrace topography favored a natural flora of deciduous forest, comprising various open to fairly dense stands. The canopy height would have been around 15 meters in drier areas, and up to 25 meters where moisture conditions permitted (Whitmore, 1984).

Non Nok Tha is an archeological site in Khon Kaen Province, northeastern Thailand. The locality lies in a piedmont area, near a sandstone monadnock at a confluence of two tributary streams. Proximity of the locality to the hill and to the stream provides for accessibility of both prehistoric and present villagers to several resource zones, extending from the river bottomland (175-205 meters elevation) to mountain top forest (500 + meters elevation) (Higham, 1975). The archeological site is a low mound, with cultural deposits spanning the time between *ca* 4000 BC and a few hundred years BP, with a gap throughout the first millennium AD (Bayard, 1972; Higham, 1989). Rice is evident in archeological context at Non Nok Tha from the earliest occupation, suggesting rice harvesting and cultivation by early inhabitants. Faunal remains include aquatic (fish and turtle) and mammal (pig, deer, cattle, dog, and water buffalo) species

(Bayard, 1972; Higham, 1975), indicating the exploitation of resources available in several ecological zones of the immediate surroundings.

Ban Chiang, another archeological site in the Songkhram Valley of northeastern Thailand, was continuously occupied from the fourth millennium BC to the early Christian era. Faunal remnants at this site has been analyzed by Higham and Kijngam (1982). Numerous land snails found in archeological context suggest the presence of shaded woodland near the prehistoric occupation area, a preferred habitat for these molluscs. The presence of fresh water gastropod species confirms that swamps with permanent water existed. Several species of bivalve shellfish occupying a habitat with clear, slow-moving, permanent water were present. The remains of wild mammal species include hare, small Indian civet, mongoose, muntjak, brow-antlered deer, cattle, pig, rhinocerus and tiger; most of them are found in deciduous forest. From these faunal inferences, Ban Chiang would have been located within the reach of slow-moving, clear streams, and some bodies of permanent water during prehistoric occupation. The low terrace location is prone to flooding with monsoon rain and is thus suitable for rice cultivation. The middle and high terraces immediate to the locality would have been covered with fairly dense stands of deciduous forest.

Malarial ecology: The inland areas of southeastern Asia would have been covered almost entirely with evergreen and monsoonal forests during the early Holocene. With the development of agriculture, beginning in the fourth millennium BC, man would have substantially changed his natural environment; Forests were progressively cleared and early farmers were tied to these man-made habitats. An agricultural environment, associated with the sedentism and higher densities of human population, as well as with the modifications of natural environment by man, created a new mode of malarial transmission.

The principal vectors of human malaria common to forest fringes on mainland southeastern Asia are the *An. dirus* complex, *An. minimus* Theobald, and *An. maculatus* Theobald. The geographic distribution of the first species complex was outlined earlier. *Anopheles minimus* has a very wide distribution in Asia; its range extends from India across mainland southeastern Asia, down to the Thai-Malaysian border, and north across China (up to 30°N latitude) to Taiwan and Rukyu islands,

Japan (Harrison, 1980). *Anopheles minimus* does not penetrate far into the equatorial rain forest zone of Malaysia. *Anopheles maculatus,* itself a complex of several morphologically-cryptic species, occurs throughout the Oriental Zoogeographic Region, including the equatorial tropical rain forest zone (Upatham *et al,* 1988).

The ecology and biology of the *An. dirus* complex have been partly described. Usually, the female mosqitos moved out of their daytime resting places in the forest as a mass flight to attack people in a village at the forest fringe (Scanlon and Sandhinand, 1965; Rosenberg, 1982). The peaks of nocturnal biting activity vary with species from early in the evening to late at night (Baimai, 1988). Population density shows a distinctive correlation with rainfall pattern. Rosenberg (1982) reported that attacks by *An. dirus* began after rainfall exceeded 5 cm per month and stopped when less than 5 cm fell; similar observations have also been reported for the much higher prevalence of *An. dirus* mosquitos during the monsoonal season (July-November), when breeding places in the forest proliferate, than during the dry season (December-June) (Scanlon and Sandhinand, 1965; Ismail *et al,* 1974).

An. minimus is known as an inhabitant of hilly regions with small, cool, clear-water streams. The larvae and immature adults of *An. minimus* can usually be collected from aquatic habitats (stream margins, rock pools, sand pools next to streams, seepage pools and springs) associated with the fringe or edge of primary or secondary bamboo forests, secondary wet forests, secondary scrub and secondary deciduous forests (Harrison, 1980). The species has been reported as primarily anthropophilic; it usually bites man indoors (endophagic), and in some cases rests indoors (endophilic) as well (Griffith, 1955; Ayurakit-Kosol and Griffith, 1956; Griffith *et al,* 1957; Scanlon *et al,* 1968; Chow, 1970; Harrison, 1980). Recent studies, however, indicate behavioral changes of *An. minimus* towards zoophilic and exophagic in areas where DDT has been applied (Ismail *et al,* 1974, 1975; Ratanatham *et al,* 1988). Densities of *An. minimus* vary from month to month and are associated mostly with the availability of its breeding places. Ismail *et al* (1974) reported from forest fringe areas near perennial streams in northern-central Thailand that the species appeared in high densities at the beginning (November) and remained at high density for the major part of the dry season

(December-February). The density dropped during the later part of the dry season (March-April). A second peak of high density appeared in the earlier part of the rainy season (May-June), then declined to reach the lowest density at the second half of the rainy season (August-September). These authors explained the first drop in population density of *An. minimus* by the partial drying up of, and the second drop, by the washing out of mosquito breeding places. Rathanatham *et al* (1988) found that *An. minimus* had longer life expectancy in the cool season than during other seasons, sugesting the greatest ability of this mosquito species to transmit malaria during the cool season (November-January). *Anopheles minimus* bites man both indoors and outdoors from dusk to dawn, with a tendency towards earlier biting (Ismail *et al*, 1974; Ratanatham *et al*, 1988).

The *An. maculatus* complex is found predominantly and abundantly in forested and foothill areas. It occupies the same breeding habitats as *An. minimus* (Ismail *et al*, 1974, 1975, 1978; Upatham *et al*, 1988). All members of this species complex tend to exhibit a zoophilic, as well as exophagic, biting behavior (Upatham *et al*, 1988). They feed at all hours of the night, with a peak between 2100 and 2400 hours for the Malayan species (Sandosham and Thomas, 1983), and around 1900 hours for the species found in central Thailand (Upatham *et al*, 1988). The ability to transmit human malaria is substantially variable within the mosquito complex. Species from the equatorial tropical forest zone of Malaysia are very efficient malarial vectors, with natural infection rates as high as 10% to 15% (Sandosham and Thomas, 1983). Negative sporozoite infections, however, have been consistently reported for this mosquito species from elsewhere in mainland southeastern Asia (Gould *et al*, 1966; Eyles *et al*, 1964; Ismail *et al*, 1974; Upatham *et al*, 1988).

When the *An. dirus* complex, *An. minimus* and *An. maculatus* complex are compared for their roles in transmitting human malaria, the first is the most efficient, followed by the second; the last species complex has been incriminated as a principal malarial vector only in the equatorial tropical forest of Malaysia. The sporozoite rates have been reported as consistently much higher for the *An. dirus* complex than for *An. minimus* (Eyles *et al*, 1964; Scanlon and Sandhinand, 1965; Ismail *et al*, 1974). For example, Scanlon and Sandhinand (1965)

found significantly higher sporozoite- and biting-rates for *An. dirus* (8.7% and 20.7 bites/man/night respectively) than for *An. minimus* (2.5% and 4.9 bites/man/night respectively) from the same study area in Thailand. In captivity, female *An. dirus* mosquitos fed on patients with *P. vivax* and *P. falciparum* infections reached the infective stage in 11-12 and 14-18 days, respectively. Parallel feedings by *An. minimus* and *An. maculatus* were not successful, either because of failure of the mosquitos to feed, or by the death of vectors before the parasites reached an infective stage (Gould *et al*, 1966).

Ismail *et al* (1974) found that malaria was endemic throughout the year among villagers in the northern part of central Thailand. The period of high transmission coincides completely with the season of *An. dirus*, and partially with the wet season of *An. minimus*; the low transmission rate during the dry season (November-March) could be maintained primarily by the *An. minimus* mosquito. The results are illustrated in Fig 6. The study area was located at the forest fringe, close to perennial streams, quite comparable to a typical location of early agricultural villages in mainland southeastern Asia. It is plausible, therefore, that malaria was endemic all year round among middle Holocene villagers, with the highest transmission during the rainy season.
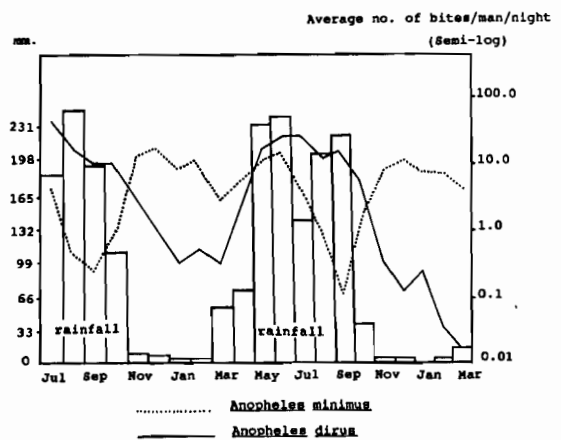

Fig 6–Seasonal Prevalence of Anopheles dirus and *An. Minimus* at Forest Fringe (Source: Ismail *et al*, 1974).

Coastal areas

Human ecology: Tropical seas of southeastern Asia are known to be the richest in the world in their coastal and marine faunal resources; almost all tropical fish species, about 6,000 species of mollusc and 100 endemic genera of decapod crustaceans (crabs, lobsters, etc) inhabit the area (Ekman, 1953; Dunn and Dunn, 1977). There are several different types of shallow marine biotopes that would have been available for prehistoric human occupations and resource exploitation: rocky shores, sandy shores, coral reefs, muddy shores, mangrove swamps and estuaries. The ecological characteristics of these biotopes have been elaborately reviewed and discussed by Sopher (1965) and by Dunn and Dunn (1977). Human sea voyages in southeastern Asia, probably associated with coastal occupation and adaptation, began at least 35,000 - 40,000 years ago (Kirk, 1981). Rises of sea level in post-glacial times, resulting in considerable lengthening of the shoreline and in land-mass reduction, simultaneously increased the availability of coastal resources, and the pressures for cultural adaptation to a coastal environment.

Archeological evidence of prehistoric human coastal and marine adaptations in southeastern Asia comes principally from occupation sites in formerly coastal caves and open coastal areas. Assemblages recovered from several cave sites, such as those from Lang-Rongrian rock shelter in southern Thailand (Anderson, 1986, 1989), from Niah Caves in Sarawak (Harrison, 1972), and from Bukit Chuping in Peris, Malaysia (Collins, 1938; Dunn and Dunn, 1977), usually show mixed inland and marine oriented economies during the early Holocene. Because these cave sites are now located well inland, marine and coastal resources would have easily been accessible to prehistoric dwellers only briefly during early and middle Holocene marine transgressions, when the sites were less distant from sea shores than at present. Shell middens in open coastal areas are found in northeastern Sumatra, Malaya, central Thailand and coastal Vietnam, all dating subsequent to the fifth millennium BC (Dunn and Dunn, 1977; Higham, 1989). Cultural layers of these open sites are usually associated with stone tool assemblages with strong Hoabinhian affinities (Dunn and Dunn, 1977; Higham, 1989).

The relative paucity and recency of prehistoric records of human marine and coastal adaptations in southeastern Asia is explicable in the light of post-Pleistocene sea level changes. The rise of sea level by as much as 150 meters in post-glacial times drowned all the late Pleistocene coastal sites; temporary marine transgressions by rises of sea level during the middle Holocene would have eliminated most of the open coastal sites occupied prior to the fifth millennium BC.

The importance of coastal habitats in prehistoric human adaptation is twofold. First, the coastal sites were strategic locations for certain valuable resources of exchange, such as sea shells. Such sites would therefore have been attractive for prehistoric occupations. Sea shells and beads made from them are commonly found in archeological context of middle Holocene occupations (*ca* 6,000 - 3,000 BP) in several remote inland areas, such as northeastern Thailand (Higham, 1989), and could only have reached there by means of exchange. Second, there is strong evidence that coastal plains, particularly those associated with both mangrove and estuarian environments, are rich and stable resource zones, capable of supporting sedentary human occupation. The best example comes from Khok Phamom Di, an extremely large shell midden in central Thailand, which has been studied by Suchitta (1980) and Higham *et al* (1987). The site is now located several kilometers inland, but it would have been situated on a coastal barrier accessible to mangrove-fringed shore, as well as to estuarian environments and fresh water swamps, during prehistoric times. The environment of the area would have alternatively changed between brackish and fresh water conditions, with fluctuations of sea level in the middle Holocene. This site clearly shows a transition from sedentary marine-oriented towards sedentary agricultural economies of the inhabitants between 2000 and 1400 BC. Also, several archeological sites in coastal Vietnam (Phoi Phoi, Phai Nam, and others) have yielded numerous polished stone hoes and sherds, evidence for primitive agriculture in the fourth millennium BC (Ha Van Tan, 1977; cited in Higham, 1989). Early coastal inhabitants could have constituted a considerable fraction of southeastern Asian prehistoric populations, particularly from the early Holocene onwards.

Malarial ecology: Several studies indicate that malarial transmission in southeastern Asia has been generally much lower in coastal than in inland

forested areas. Gould *et al* (1966) found no malarial cases in the presence of *An. sundaicus*, a mosquito known to be a malarial vector, in the coastal area of southern Thailand. Harinasuta *et al* (1974) found neither malaria cases among inhabitants nor the parasite vector, *An. sundaicus*, in mangrove areas of eastern Thailand. Wharton *et al* (1963) reported a very low parasite rate in the coastal area of western Malaya, compared with those in neighboring inland areas, where *An. maculatus* was a primary vector. Similar results were reported from Borneo, where *An. balabacensis balabacensis* and *An. leucosphyrus* were principal vectors of the forest interior (McArthur, 1947; Zulueta, 1956).

Cases of coastal human malaria in southeastern Asia have been reported from time to time. The principal malaria vector is *An. sundaicus* Rodenwaldt (Gould *et al*, 1966). This brackish water mosquito is common in coastal areas throughout southeastern Asia. It breeds prolifically in water having a salinity of between 3 and 50% sea water (Sandosham and Thomas, 1983). The usual breeding places are pools and swamps at the limits of tidal rise, where dammed up seawater is diluted by rain and seepage waters to a salinity suitable for mosquito breeding (Sandosham and Thomas, 1983). Such breeding localities are rare in nature; their proliferation is usually associated with human activities, such as the damming of tidal water and construction in the tidal zone. *Anopheles sundaicus* bites man both indoors and outdoors at night. Very low natural sporozoite infection rates (0.04% rate among 13,493 female mosquitos dissected) has been reported from Malaysia for this mosquito species (Sandosham and Thomas, 1983). Because it is a prolific breeder, enormous numbers of female mosquitos may be able to make up for low infection rates (or even for periodic epidemic outbreaks) in some coastal areas, but prevalence, depending on the availability of breeding habitats, is far from consistent. The transmission of human malaria would have been generally much lower and less uniform among early coastal inhabitants than among inland settled farmers.

Flood plains

Human ecology: The expansion of sedentary occupation onto riverine and lacustrine floodplains in mainland southeastern Asia has been extensive, and most of these areas have been continuously occupied since the beginning of the first millennium BC (Coedes, 1966, 1968). Evidence comes primarily from: (1) the Red River Delta in northern Vietnam, (2) narrow coastal plains in southern Vietnam, (3) the Mekong River Delta in Cambodia and southern Vietnam, and (4) the Chao Phya River Delta and some inland valleys in Thailand. Rice production intensified considerably in these lowland areas from the mid first millennium BC onwards (Higham, 1989). The intensification of rice production would have allowed population growth, reflected in the increasing number of occupation sites during late prehistoric times in all these areas. Between the last few centuries BC and the early first millennium AD, there was a general trend of change from local autonomy towards political centralization among flood plain communities, along with the development of extensive maritime and long-distance inland exchanges.

Malarial ecology: The upland river valleys in mountainous areas of upper southeastern Asia had been highly endemic for malaria, before malarial control or eradication programs were launched (Pons, 1943). For example, malaria was hyperendemic in the Ping River Valley of northern Thailand in 1949, with a spleen rate in children of 63.8% and a slide positive rate of 47.3% reported (cited in Jacobs *et al*, 1983). The principal malarial vectors were the *An. dirus* complex and *An. minimus*.

On the other hand, the broad lowland flood plains formed by several major rivers, such as the lower Chao Phya Valley in central Thailand, the Red River Delta in northern Vietnam, and the Mekong River Delta in southern Vietnam, have been relatively free from human malaria. Most of the important malarial vectors: the *An. dirus* complex, *An. maculatus* complex and *An. minimus*, are especially rare. The common mosquito known to transmit human malaria on lowland floodplains of southeastern Asia is *An. aconitus* Donitz, a species occurring throughout the Oriental Zoogeographic Region (Harrison, 1980). The mosquito is abundant on the plains but not in dense forest (Scanlon *et al*, 1968). Natural breeding places of this mosquito are primarily grassy marshes with slow, clear, running water and along open streams and rivers with grassy margins. The species also breeds prolifically in rice fields (Harrison, 1980). *Anopheles aconitus* is primarily zoophilic, exophilic and exophagic (Wharton, 1953; Chow *et al*, 1960; Reid, 1968; Harrison, 1980). Natural sporozoite

infection has been reported as very rare, 1/3226 female mosquitos dissected (Sandosham and Thomas 1983). The species has been suggested to be a malarial mosquito vector maintaining very low parasite rates (3.4% and 0.3% for *P. vivax* and *P. falciparum,* respectively) among populations in central Thailand (Gould *et al,* 1967). Generally speaking, human communities on lowland riverine floodplains of southeastern Asia, substantially proliferating from the first millennium BC onwards, would have been relatively free from malaria.

CONCLUSION

It is likely that most of contemporary simian malarias originated in tropical forests of southern and southeastern Asia from hepatocystis or probably a quartan plasmodiid ancestor, reaching tropical Asia from Africa in the Miocene. The parasites could have well survived during Pleistocene dessications in forest refuges with the presence of appropriate vectors in the *Anopheles leucosphyrus* group and of numerous species of their vertebrate hosts. Man extensively occupied tropical forests of southeastern Asia subsequent to the last glacial maximum and would have received zoonotic simian malarias; evidence for monkey-man contact for the disease via the biting of *An. dirus* mosquitos is obvious in forests on the mainland. Human malarias could have spread from southeastern Asia, and have become common in most of tropical Old World from the middle Holocene onwards.

The ecology of malarial transmission was truly diverse among prehistoric inhabitants of southeastern Asia. The abundance of the most efficient malarial vectors in the *An. dirus* complex could have been able to maintain low endemic malaria among early Holocene forest dwellers with low densities and sparsely distributed populations. The disease would have been holoendemic among middle Holocene settled farmers inhabiting forest fringe areas, with the presence of the *An. dirus* and *An. minimus* mosquitos. The transmission of human malaria should have been generally much lower and less uniform among early coastal inhabitants with the presence of *An. sundaicus* than among inland settled farmers. Malaria would have been practically absent among flood plain inhabitants in late prehistoric times with the lack of efficient mosquito vectors.

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