

ECOLOGY OF ANOPHELES VECTORS OF MALARIA IN THE ORIENTAL REGION *

par

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This review covers the period between the Seventh International Congresses of Tropical Medicine and Malaria and the end of 1967 ; and the Oriental region as outlined by Christophers (1933), excluding the Philippines.

SUBGENUS ANOPHELES

Contains few important malaria vectors in the Oriental region. We know little or nothing concerning the habits of many the forest-inhabiting species in the subgenus, such as the *aitkenii* group (REID, 1965), *annandalei*, *sintonoides*, etc. Many species, particularly in the relatively ancient series *Myzorrhynchus* are almost always strongly zoophilic. A number of difficult species complexes are included in the subgenus, making it difficult to evaluate early ecological observations (for example those in COVELL, 1944) in some cases. Even when the complexes have been resolved recently (e.g., REID, 1962 ; REID, 1965) the results may not apply to all populations of the complexes in the region.

A. hyrcanus complex — Most are strongly zoophilic, and the immature stages are found in swampy areas or rice fields, generally away from forests. *A. sinensis*, one of the most abundant, has long been reported as a vector in South China, but many of these reports must refer to *lesteri* (vide infra). Aside from *lesteri*, *sinensis* appears to occur in several forms in China, distinguishable best perhaps by egg variations (MA, 1966). In some areas it is strongly zoophilic, but it appears to be the human malaria vector over the open plains in a large part of China (Ho, 1966). It is reported to rest primarily in cattle sheds in some areas (Liu et al., 1960), but it moves up from buildings in Canton (Ho et al., 1965) and rests in creek banks and caves, where females of all physiological ages may be found simultaneously. Ho, Jung and Ko (1965) found that the number of parous females increased as the year progressed, and from combined longevity and population peaks showed that October was the most dangerous month in the Canton area. There are scattered reports of *sinensis* as a vector elsewhere in the region, but none of great importance.

A. lesteri is strongly anthropophilic in parts of China (Ho, 1965) and is probably an important vector wherever abundant in South China : although it is not a vector in the Philippines. In Malaya, Thailand, South Vietnam and Borneo, *lesteri* is represented by its subspecies *paraliae*, largely confined to coastal areas, and not a vector. Nothing

* Communication présentée au Congrès de Téhéran (7-15 septembre 1968), section B.2.2.

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is known about the area where the two subspecies meet, nor the precise limits of the area within which *lesteri* is a vector. In Thailand, *paraliae* is relatively uncommon, restricted in distribution, and biting man in very small numbers. MA (1966) and FENG (1964) reported that several forms, apparently all zoophilic, might occur within *lesteri* in China, but it is not known how these relate to other members of the complex from elsewhere in the region. Overall, less is known concerning the habits of *lesteri* than of *sinensis*. The biting activity peak appears to be later (0100 to 0300, as opposed to 1900-2100 for *sinensis*), while the seasonal population peak occurs earlier.

A. barbirostris complex — Characterized recently by REID (1962) for Malaya and WATTAL *et al.* (1962) for India, but much taxonomic work remains to be done for other areas.

A. barbirostris — Where this member of the complex occurs alone, or where it can be clearly identified, it is not a significant vector. In Thailand for instance (SCANLON *et al.*, 1968) it is common in a variety of biotopes, but rarely attacks man, and despite one early record of a gland-positive individual it is not regarded as a vector. BRUCE-CHWATT *et al.* (1966) show great variations in the human blood index for *barbirostris* (*sensu lato*), but it is of course impossible to evaluate these data without knowing the identity of the member of the complex involved.

A. campestris (the « dark-winged form of *barbirostris* » of earlier workers) is a vector on the western coastal plain of Malaya, where larvae are found in still, partly shaded, deep water. Adults bite man in preference to cattle, and in larger numbers indoors than outdoors. MOORHOUSE and WHARTON (1965) showed an indoor-outdoor biting ratio of 1 : 4.4 in simultaneous catches in Malaya. Such house-frequenting habits led to its complete disappearance from a sprayed area of coastal Selangor, Malaya (MOORHOUSE and CHOOI, 1964), while co-existing but zoophilic *barbirostris* was essentially unaffected. In the plains of Thailand, however, a morphologically indistinguishable *campestris* population was less attracted to man, and probably not a vector, though somewhat endophilic (GORDON *et al.*, 1967).

A. donaldi is a dominant member of the *barbirostris* group in Borneo, from which *barbirostris* (s.s.) and *campestris* appear to be absent, often being among the most common anophelines in houses at night. In Malaya (MOORHOUSE and WHARTON, 1966) *donaldi* migrates from the jungle to the vicinity of villages at night (2200-2400 hours) where it may enter houses to feed, although most feeding takes place outdoors. In the jungle, feeding occurs all day, but with well defined peaks. Analysis of the parous/nulliparous ratio at different portions of the biting cycle showed no significant differences. It also appeared possible that some of the infections found were not of primate origin (MOORHOUSE and WHARTON, 1965).

A. umbrosus complex — The dozen or so species of this complex are largely jungle forms ranging from Assam to the Moluccas, the largest number being found in the evergreen forests of Malaya, Sumatra and Borneo. Early records of malaria transmission by « *umbrosus* » (e.g. COVELL, 1944) should be treated with caution, both because of later taxonomic clarification of the group, and their proven rôle as vectors of non-human plasmodia.

A. umbrosus is common in swamp-forest areas of Malaya with dark acid waters under heavy shade. Adults will attack man freely in the forest by day, and at times will enter houses or manbaited traps at night. High oocyst and sporozoite rates have been found, but most of the infections have probably been with *Plasmodium traguli* of the mouse deer (WHARTON *et al.*, 1963); although some transmission of human infection probably also occurs where conditions are suitable. Infections in two other species of the complex, *baezai* and *roperi* are probably all of mouse deer origin.

A. letifer often occurs with *umbrosus*, but the larvae are found in shaded or sunlit waters on the edge of the swamp forest. Adults do not bite freely during the day, but will feed on man outdoors at night, or enter houses in smaller numbers (MOORHOUSE and WHARTON, 1965). This species is undoubtedly a human malaria vector in some places in Malaya (WHARTON *et al.*, 1963), with sporozoite rates of 0.2. to 0.8. per

cent ; but it can also be common without apparent transmission. (MOORHOUSE 1965) found it strongly attracted to chickens and ducks, and since it also transmits mouse deer malaria its feeding patterns appear to be particularly complex.

A. whartoni, very similar in appearance to *letifer*, appears to be a minor vector in limited areas of eastern Malaya. This occurs during periods of unusual abundance, which may occur only once every few years and last for only a few weeks (WHARTON, 1960).

SUBGENUS CELLIA

Is divided into several well defined Groups (CHRISTOPHERS, 1933) and the species in these generally form a number of species complexes.

Group Neomyzomyia.

A. leucosphyrus complex — *A. balabacensis* is probably the most important human malaria vector in many forested areas of the region, as far west as Assam, eastward to Hainan, where it appears to be quite common (SHENG et al., 1963). Gland positive individuals have been found on Hainan wherever dissections were made (HO, 1965). This has also been true in Thailand (SCANLON and SANDHINAND, 1965), Cambodia (EYLES et al. 1964), northern Malaya (SANDOSHAM et al., 1936) and elsewhere in its range. It is highly anthropophilic and its high infection rates make it a dangerous vector. One of us (John E. SCANLON) has encountered transmission several times in Thailand jungles at vector levels almost too small to measure by human biting tests.

Females are strongly exophilous and exophagous, but they will enter shelters to feed, rarely remaining long and returning to the jungle during the day. Thus they avoid much contact with sprayed surfaces and a good deal of the contact with man may take place away from dwellings entirely. In most of Thailand (SCANLON and SANDHINAND, 1965) and in Cambodia (EYLES et al., 1964) *balabacensis* feeds largely in the hours after midnight ; but in other parts of Thailand (GOULD, 1968) and northern Malaya the peak of feeding comes not long after dark. Specimens from these areas exhibit no morphological differences.

Females feed readily on non-human primates, and some high primate blood indices, such as those given by BRUCE-CHWATT et al. (1966) for Sabah doubtless include feeds on non-human primates. *A. balabacensis* is readily attracted to simian baits (EYLES et al., 1964) on the ground or in the canopy. Larvae are found in small water collections in or near the jungle, in streamside pools, or, in Vietnam at least, in rock holes (QUY and QUE, 1967). The relative inaccessibility of the breeding sites and the exophilic and exophagic habits of *balabacensis* make its control difficult. Residual spraying of dwellings with complete walls offers some protection from indoor biting, but this type of construction is rare in most forested areas where it is a vector. CHENG (1967) investigated the effect of residual spraying in varying patterns of construction in Sabah, spraying both inner and outer surfaces, with generally discouraging results.

A. leucosphyrus (s.s.) is a vector of human malaria in Borneo, with habits much like those of *balabacensis*. In peninsular Malaya, however, it is not a proven vector, perhaps because of its small numbers, or its preference for feeding on monkeys in the canopy (WHARTON et al., 1964).

These two species, and other members of the *leucosphyrus* complex, will be discussed further below in connection with simian malaria.

Group Myzomyia.

A. minimus is an extremely important vector in much of the hill areas of the region ; as a rule it is a vector wherever encountered in numbers. Fortunately, it has

been very amenable to residual spraying almost everywhere, due to its endophilic and endophagic habits. Much of the basic ecology of *minimus* was elucidated by Muirhead-Thomson (1951), and in view of its importance surprisingly few details have been added since then. Precipitin tests (BRUCE-CHWATT et al., 1966) have generally shown a high proportion feeding on man, but some samples (e.g. Cambodia, Taiwan) show extensive cattle feeding. QUY et al. (1963) noted « temporary diversion » of *minimus* to stables in South Vietnam in sprayed areas, but their data are too incomplete to permit full evaluation. Later, QUY and QUE (1967) reported a far higher number of *minimus* feeding on man than on cattle. In both South and North Vietnam (LYSENKO and NGY, 1965) *minimus* is still a dangerous vector in hill and plateau areas as unsettled conditions have interrupted control operations. LYSENKO and NGY (1965) found epidemiologically dangerous females (based on age grading) for eight months of the year in North Vietnam, and TOMASZUNAS (1966) reported that *minimus* ceased to rest on sprayed walls in that country, thus avoiding insecticide contact.

GOULD (1967) reported increased outdoor biting, exceeding indoor biting, by *minimus*, in a Thailand locality which had been sprayed for some ten years. In other sprayed areas of Thailand it has essentially disappeared, as it has from the control area in Perlis, Malaya (SANDOSHAM et al., 1963) near the Thai border — the only portion of Malaya where *minimus* occurs.

A *varuna*, closely resembling *minimus* is reputed to be a vector in parts of India, innocuous in other parts. This may be partly due to taxonomic confusion, as forms resembling *varuna*, *filipinae* and other species have been found in populations of what is almost surely *minimus* in Thailand. The same may be true of reports of *varuna* and *minimus flavirostris* from Indonesia. This entire complex of species is badly in need of taxonomic study before ecological observations can be meaningful.

A. jeyporiensis candidiensis, generally more common at higher altitudes than *minimus*, is an important vector in Vietnam (QUY and QUE, 1967) and South China (HO, 1965). HO (1965) found it highly anthropophilic on Hainan, with a high sporozoite rate. BRUCE-CHWATT et al. (1966) reported almost no human blood meals for *candidiensis* in India, but a high human blood index in Nepal. Both *jeyporiensis jeyporiensis* and *j. candidiensis* are said to be vectors in South Vietnam, but only *candidiensis* has been found in Thailand (SCANLON et al., 1968).

A. aconitus is a highly variable species, with forms within well studied populations which may be extremely close to *minimus*, *flavirostris* and *varuna*. It is much more widely distributed than *minimus*, from coastal areas to hills and plateaus. It is strongly zoophilic in most areas (BRUCE-CHWATT et al., 1966), but is an important vector in parts of Java and Sumatra, Indonesia (SOERONO et al., 1965) and more recently gland positive specimens were found in a limited malaria focus just north of Bangkok, Thailand (GOULD, 1967). This is one of the few malaria vectors to have developed resistance to both D.D.T. and dieldrin. SOERONO et al. (1965) reported that this was not accompanied by an increase in transmission, presumably because the parasite reservoir had been reduced sharply before insecticide resistance developed. In the areas in question biting still took place indoors as well as outdoors, at high levels if cattle were in the vicinity. In experimental huts D.D.T. reduced the total entry of *aconitus*, but not the portion leaving unfed.

A. culicifacies was an important vector in many areas of India prior to the malaria eradication campaign. BRUCE-CHWATT et al. (1966) reported high rates of feeding on man in unsprayed areas, with the human blood index dropping sharply in sprayed areas. On the whole, however, *culicifacies* appears to be quite zoophilic, with a poor infectivity rate compared to other vectors in India, transmission depending on the presence of large numbers (SINHA and MISHRA, 1965 ; PAL, 1964). Where spraying has been effective, *culicifacies* population have tended to drop to low levels, followed by slow rises almost to pre-treatment levels, often without concomitant rises in malaria transmission. Insecticide resistance has also appeared in *culicifacies* populations in India, without widespread reappearances of malaria, probably due to large increases in the

proportion of the population exhibiting exophilic behaviour (PAL, 1964), reduced longevity of the resistant strains (SHALABY, 1965) and increased irritability.

A. fluviatilis, another important Indian vector, seems to occur in several physiological races, as suggested some years ago (COVELL, 1944). Densities of *fluviatilis* dropped after spraying in much of South India, while elsewhere populations remained high despite sustained spraying, presumably because *fluviatilis* is primarily zoophilic in such areas (PAL, 1964). It has been suggested (BRUCE-CHWATT *et al.*, 1966) that such apparent effects on feeding patterns in the fact of spraying as appear in *fluviatilis* may persist after withdrawal of spraying, an effect which should be observed carefully over a protracted period. Observations on apparent changes in *culicifacies* and *fluviatilis* feeding and resting patterns in India are among the best made in the region thus far. But even there more detailed studies are needed, along the lines suggested by BRUCE-CHWATT *et al.* (1966), GARRETT-JONES (1964) and GARRETT-JONES and GRAB (1964).

Group Pseudomyzomyia.

A. sundaicus is the most important Oriental vector in this Group. It is a coastal species, from the Bay of Bengal eastward to Borneo and the Celebes. Its distribution is patchy, but it tends to be a vector wherever present in large numbers. It is more strongly associated with man, and a more important vector, in Java than in Malaya, Borneo or adjacent areas. Sporozoite rates tend to be very low, but biting rates of over 100 per night are not uncommon and compensate for the low sporozoite rates, which may be due to a low average length of life. In Malaya, MOORHOUSE (1965) found *sundaicus* a sporadic house refter, but highly exophagic and zoophilic. Similar habits have been observed in Thailand (GOULD, 1968) where only one house in a group may yield *sundaicus*, and that one not regularly. In addition to MOORHOUSE's (1965) report of extreme zoophilism in Malaya, BRUCE-CHWATT *et al.* (1966) showed a low human blood index for small samples from India, a high rate for Indonesia. The patchy distribution of *sundaicus*, probably due to the requirements of most larval populations for particular types of brackish pools, makes the assessment of populations difficult. In the laboratory *sundaicus* breeds readily in fresh water, and fresh water inland populations are known, particularly from Sumatra. *A. sundaicus* is related to the African *gambiae* complex, which also contains salt- and fresh-water forms, and for this reason *sundaicus* and its closely related Oriental relatives deserve much additional taxonomic and ecological study.

Group Neocellia.

A. maculatus is widespread in the Oriental region, and is the principal vector in all cleared hilly land in Malaya, sporozoite rates averaging about 0.5 per cent; but it is unimportant, or not a vector in much of its range, e.g., in most of Thailand and in Borneo. This variation in vector status seems to be due to geographical variation in the degree of attraction to man. In Malaya, although more attracted by cow than man (WHARTON, 1951), it continues to enter houses to bite man, even when cattle are present nearby, and is more attracted to man than other local vectors (except *campestris* and *balabacensis*). But in Borneo (de ZULUETA and LACHANCE, 1956), Cambodia (EYLES *et al.*, 1964) and Thailand (SCANLON *et al.*, 1968) it is much more strongly attracted to domestic animals. Adults rest outdoors by day and at night bite for preference outdoors. In Malaya (MOORHOUSE and WHARTON, 1965) the majority bite after about 2200 hours. If biting indoors, they usually do not rest on the walls until after they have fed (REID and WHARTON, 1956). There is only a slight difference in the parous rates among females captured at various times of the biting cycle (MOORHOUSE and WHARTON, 1965).

In Malaya larvae are found in large numbers in clearings in hill-forest made by Aborigines who practise shifting cultivation. In fact, malaria due to *maculatus* is lar-

gely a man-made disease, and before man began to clear the Malayan forest *maculatus* must have been a rare species. Morphologically *maculatus* is a variable and polymorphic species (REID *et al.*, 1966) and the relation of this morphological variation to the variation in vector status should be investigated. In this connection, a knowledge of where the vector form in Malaya gives way to the non-vector form in Thailand would be relevant. The species is often very abundant in northern Thailand and in Vietnam (QUY and QUE, 1967) in both of which areas shifting cultivation is practised by hill tribes, but these large populations are not accompanied by *maculatus*-borne malaria as seen in Malaya.

A. stephensi continues to pose a problem in some urban areas of India (PAL, 1964), where it often breeds in wells and similar habitats. The type form is reported to be more anthropophilous than *stephensi mysorensis*, which appears to be more rural. It is difficult to assess blood feeding indices (BRUCE-CHWATT *et al.*, 1966) or other ecological data, since the varieties are separated on differences in the eggs and it is often difficult to be sure which form is cited. The assumption that all urban populations can be referred to the type form needs additional verification. Examination of colonized strains from India, Pakistan and Iran at the Walter Reed Army Institute of Research and elsewhere indicate that the egg character may not be reliable for separating the varieties, despite the apparent behavioral differences in the field. *A. stephensi* is a particularly useful laboratory species for transmission of a wide variety of human and lower primate malaria parasites.

Preliminary findings of TARIQ (1967) indicate that another *Neocellia* species, *superpictus*, may be the vector of human malaria in the Gilgit Agency, West Pakistan which is unusual for the extreme altitude (up to 12,200 feet) at which it was encountered. It is still too early to assess the ecological factors involved, but cases were seen in children who had never left villages ranging from nine to over twelve thousand feet in elevation.

SIMIAN MALARIA. —

Some of the more interesting and potentially important malaria research in the Oriental region recently have dealt with malaria in lower primates, and its transmission to man in jungle areas. Following the first accidental laboratory transmission of *Plasmodium cynomolgi bastianelli* to man by mosquito bite (EYLES *et al.*, 1960), a large scale field effort was made in Malaya to determine the possible significance of the finding in nature. This culminated in the detection of a natural infection of *P. knowlesi* in man (CHIN *et al.*, 1965). During these studies a large number of lower primate malaria parasites were detected, and the natural cycles determined for most of them (WHARTON *et al.*, 1964; EYLES *et al.*, 1963; CHEONG *et al.*, 1965). By 1965, it was evident that simian infections were widespread in Malaya, and that they were transmitted primarily, if not entirely, by mosquitoes of the *leucosphyrus* complex.

The first simian malaria vector detected was *hackeri*, originally thought to be a hill-forest species which had become adapted to Nipah palm plantations on the coast, the larvae being found in water collected at the base of the fronds. Five plasmodia have been isolated from *hackeri*: *Plasmodium knowlesi*, *coatneyi*, *cynomolgi*, *fieldi* and *inui* (WHARTON *et al.*, 1964). It is, however, hardly ever attracted to man (WHARTON *et al.*, 1964) and seems unlikely to transmit these parasites to him. *A. hackeri* also occurs in Thailand and Indonesia, but its role as simian malaria vector has not been investigated in those areas.

A. leucosphyrus transmits *P. inui* in hill-forest where, however, its feeding activity is largely limited to the canopy, posing little danger to man. Another hill-forest form, *balabacensis introlatus*, transmits *P. cynomolgi* and *fieldi* among simians, but like *leucosphyrus*, it is relatively uncommon in Malaya and it feeds rarely on man.

More recently *P. cynomolgi* and *inui* were isolated from *balabacensis balabacensis* in monsoon forest near the Thailand border (CHEONG *et al.*, 1967). Given the high vector efficiency of *balabacensis* and its propensity for feeding on man or monkeys, at ground level or canopy levels the possibility of fairly frequent exchange of parasites

in a human-mosquito-lower primate system seems evident, wherever suitable conditions occur. Simian malaria parasites have long been known from India, and recent isolations of several species have been made from monkeys (RAMAKRISHNAN and MOHAN, 1962; PATTANAYAK, 1963) and from *A. elegans*, another member of the *leucosphyrus* complex (CHOUDHURY et al., 1963). Some 98 per cent of the blood meals tested from this species in Madras (BRUCE-CHWATT et al. 1966) were of simian origin, with no human blood meals detected, so there is some question as to whether man is likely to become involved in this cycle. Extensive simian infections have also been reported from Ceylon (DISANAIKE, 1965) and other portions of the region, but it is still too early to assess their full impact.

At the moment, it is impossible to determine how many infections in man may be of lower primate (monkey or gibbon) origin in the forests of Southeast Asia. Several of the species of simian malaria are morphologically extremely close to the human parasites, and the question of host-induced morphological changes must be considered as well. The possibility of detecting such infections in man in the course of routine control or eradication surveys is slight. They can best be detected by inoculation of known uninfected monkeys and exceedingly few institutions in the region are equipped for this type of work. The extent of the problem may not become evident until human malaria parasites have been largely eliminated. The immunological consequences of the introduction of parasites of lower primate origin into such a population are probably unforeseeable at this time, and beyond the scope of this review. However, at least two simian parasites are certainly readily transmissible to man and primate feeding mosquitoes are present in enough numbers to make one feel confident that the scope of the problem will grow as it becomes clearer. Detailed studies of the type reported by WHARTON et al. (1964) for Malaya are urgently needed in other areas, but it is difficult to say where the personnel and other resources for such studies will be found in the region.

REID (1968) has suggested that the human malaria parasites may have evolved in the forests of Southeast Asia from simian parasites transmitted by members of the *leucosphyrus* complex. It is a fact that most of the major vectors of the Old World belong to the subgenus *Cellia*. The vectors in the subgenus *Anopheles* in the region belong to the relatively ancient series *Myzorrhynchus*, and it may be that only a few strains of human malaria parasites will develop in these primarily zoophilic species. WHARTON et al. (1964) also noted that simian parasites developed poorly if at all in the species of subgenus *Anopheles*. If Reid's hypothesis of the origin of the human malaria parasites is correct it has far ranging consequences in terms of eradication of the disease in Southeast Asia, since it implies a very basic association of long standing. The fact that *balabacensis* and other members of the *leucosphyrus* complex may be extremely difficult to control by traditional spraying methods adds another dimension to the problem.

OTHER NEEDED WORK. —

The variation in vector status of species in various portions of their range, noted so frequently in this review, requires both laboratory and field study. Where there are morphologically distinguishable forms in different areas, the areas where the two forms meet or intergrade should be studied to see if there has been interbreeding, as was done for *balabacensis balabacensis* and *b. introlatus* in south Thailand (SCANLON et al., 1967), or whether in fact they behave as two species.

If such studies show that the two forms are interfertile then the question of why one form is a vector (e.g. *maculatus* in Malaya) and the other form not (*maculatus* in Borneo and northern Thailand) should be investigated. Differences on host preference, properly measured by trapping with human and animal baits under a variety of ecological conditions, may prove to be the commonest reason, but differences in mosquito susceptibility to local strains of the malaria parasite should also be investigated. In either case a long range objective should be to discover the mode of inheritance of such differences affecting vector status, having in mind the ultimate possibility

of ecologically or genetically replacing a vector by a non-vector form. Before this can be done properly, or the impact of control or eradication campaigns with insecticide assessed, much basic ecological data will have to be accumulated along the lines suggested by BRUCE-CHWATT *et al.* (1966) ; MOORHOUSE and WHARTON (1965) ; GARRETT-JONES (1964) ; GARRETT-JONES and GRAB (1964).

Perhaps the most striking aspect of the survey of the literature in preparation of this review is the relative paucity of such ecological data in the Oriental region, even for the major vectors. The emergence of the importance of relatively unknown exophilic vectors, and the possibility of induced exophily make the task all the more urgent. Every effort should be made now to accumulate the type of data for all of the vectors which PAL (1964) indicates would have been useful for the Indian vectors as baseline data before the eradication program was undertaken there.

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