

Systematics of Malaria Vectors

Anopheline Systematics and Malaria Control, with Special Reference to Southeast Asia

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ABSTRACT

The main function of morphological taxonomy of anophelines is to permit accurate identification of species, but infraspecific variation also is important. Species and subspecies are briefly defined, and sibling species-groups are more fully discussed. There is need to coordinate the findings of classical taxonomy and those of chromosomal taxonomy. The number of species of *Anopheles* known in the world has doubled in 30 years and now stands at about 350, but the rate of discovery of new species shows

no obvious decline. Many species-groups need further study, and knowledge of the distribution and variation of their member species is often fragmentary.

Widespread vector species show geographic variation in morphology and in vector status. Examples are given to show that a study of the correlation between infraspecific variations in morphology and vector status holds promise of future advances in malaria control.

The intention in this paper is to discuss the present status of anopheline systematics and its importance for malaria control or eradication, and after that to deal in more detail with what still needs to be done, especially the study of variation within species in relation to variation in their vector status.

Systematics and Vector Control.—It is a well-understood axiom that efficient control of an insect vector of disease is not possible unless we can recognize the vector species accurately and concentrate our efforts against that species. Since most species are recognized, and will continue to be, by their morphological characters (even if occasionally these are limited to the chromosomes), this will always be the major contribution of morphological taxonomy to vector control—to provide the means to identify individual specimens to their correct species.

This need raises the question of what we mean by species, but there is not space to enter into a detailed discussion here. It is sufficient to say that I belong with the majority of systematists who follow the biological species concept of Mayr (1942), which I like to state as follows (Reid 1965): "Species are groups of actually or potentially interbreeding populations reproductively isolated, and usually morphologically distinguishable, from other such groups." I should add that subspecies are geographically limited and taxonomically distinct units within a species, and that they usually ought not to be given formal subspecific names unless 75% or more of the individuals are morphologically distinguishable from those occurring in other parts of the range of the species.

Sibling Species Groups.—The need for accurate identification of species, if vector control is to be efficient, emphasizes the great importance of sibling species-groups. In these groups the species are so similar in appearance that morphological identification may be a difficult or slow process, although the

species in a group may differ so much in their biology that some are important vectors of human disease and others are harmless.

Species-groups of this sort are common in mosquitoes, and about half the *Anopheles* species of Malaya (by which is meant the Malay Peninsula) and Borneo belong in such groups, which also contain many of the major malaria vectors of the World. Examples of such groups are the *funestus*, *gambiae*, *leucosphyrus*, *maculipennis*, *minimus*, and *punctulatus* groups.

The evolutionary significance of sibling species-groups is not known, but clearly they must have survival value as they are so numerous and successful. Mayr (1963) suggested that perhaps the common phenotype of each group is a particularly successful one, and any considerable morphological deviations from that phenotype tend to be less successful and are selected against. Possibly in some groups, in which the morphological similarity between the species is particularly close, this may be partly due to their relatively recent origin. For example, Reid and Knight (1961) gave reasons for thinking that the *maculipennis* group is more recent than the more highly ornamented *pseudopunctipennis-lindesayi* group, or the *hyrcanus-coustani* group, in both of which the species tend to show larger or more numerous differences than are found between the species of the *maculipennis* group. If there is anything in the argument of degree of difference in relation to evolutionary age, then the *gambiae* group should be of relatively recent origin, since most of the species appear to be indistinguishable morphologically, except by their chromosomes.

Defining Species-Groups.—The species-group, like other taxonomic categories except that of the species itself, is a more or less subjective category. How to define any particular species-group and which species to include in it are matters of taxonomic judgment, just as with genera and subgenera. But unlike those

¹ Supported by a grant from the Wellcome Trust.

2 categories the species-group has no formal standing in nomenclature. This concept has the advantage that there is no need to put every species into a species-group as must be done with genera and subgenera, which avoids such an absurdity and contradiction in terms as a monotypic species-group.

In general the term "species-group" should be reserved for natural groups of very similar species where the consensus is that the concept has practical value and convenience.

The term "species-complex" has been used more or less interchangeably with species-group, but has been employed also in other senses. For example, it has been used to refer to a single polytypic species such as *Culex pipiens* L., which Mattingly (1967) called the *pipiens* complex, and which contains various named forms such as *pipiens pipiens*., *p. fatigans* Wiedemann, *p. pallens* Coquillett, and *pipiens* var. *molestus* Forskal. On the other hand, Kitzmiller et al. (1967) spoke of the *Maculipennis* complex with a capital *M* as if it were a genus, and conceived it as containing 2 groups of species in North America, thus using complex as a category of higher rank than the species group. I have tended to use species-complex to refer to suspected species-groups before they have been sufficiently analyzed to establish that the forms they contain are distinct species. Thus a few years ago it was the *A. gambiae* complex to me where now it is the *gambiae* species-group.

It may be that in those groups with the most closely related and similar looking species, such as the *maculipennis* and *gambiae* groups, one of the criteria for deciding which species should be included might be the results of crossing experiments. For example, when the degree of genetic incompatibility is so great that no eggs hatch, and examination shows that little or no development of the hybrid embryos has occurred, one might conclude that any species which proves sterile in this way when crossed with all the other species of the group does not belong in that group. But, as usual, a balance would need to be struck between genetic evidence of this sort and other evidence from morphology and distribution.

In other groups, in which the species are morphologically better differentiated, it may be that crosses would usually be completely sterile. We do not know, and clearly there is a large field for investigation here. There are several important species-groups, such as those of *A. barbirostris*, *minimus*, or *leucosphyrus* in Southeast Asia, or *funestus* in Africa (the last-mentioned closely related to the *minimus* group), which so far are defined almost solely on morphological and ecological grounds. The results of crossing the species in these groups would be of great interest and would serve as a check on the morphological taxonomy. If the chromosomes of the species could be examined at the same time this would greatly enhance the value of the work and should help to coordinate the conclusions of ordinary taxonomy based mainly on external characters and those

of cytogenetic taxonomy based on the appearance and banding of the giant chromosomes.

Cytogenetics and Classification.—At present there is danger that morphological and chromosomal taxonomy are about to get badly out of step. For example, Frizzi et al.² extended a hypothesis of Kitzmiller et al. (1967), that the *Maculipennis* group (spelled with a capital *M* as if it were at least a subgenus) had its origin in Central America and reached Europe via the Bering connection. They seem to suggest on grounds of similarities of the banding pattern of the salivary chromosomes that *A. nigerrimus* Giles of the *hyrcanus* group and *A. barbirostris* Van der Wulp, in India, have evolved from the palaeartic *maculipennis* group, which is itself an offshoot of the North American *maculipennis* group. But the evidence of morphology and distribution (Reid 1968, p. 51) strongly suggests that the *hyrcanus* and *barbirostris* groups are of much older origin. Both belong to the relatively ancient *Myzorhynchus* series of subgenus *Anopheles*, of which the Central American counterpart is the *Arribalzagia* series to which *A. vestitipennis* Dyar and Knab and *neomaculipalpus* Curry belong. Kitzmiller et al. (1967) found that these last 2 species also have chromosome patterns like those of the North American *maculipennis* group, but so also do 2 other Central American species, *pseudopunctipennis* Theobald and *hectoris* Giaquinto-Mira, which belong to the quite different *Anopheles* series which includes *maculipennis* Meigen (Reid and Knight 1961). Almost certainly, as Kitzmiller et al. recognized, this similarity in the banding pattern of the chromosomes in all these species is a character of the subgenus *Anopheles* as a whole, rather than of the *maculipennis* species group as such. Quite different patterns are found in the few species of the subgenera *Nyssorhynchus* and *Cellia* that have been examined.

Numbers of Species of Anopheles.—One would have hoped that by now we would know the great majority of species of *Anopheles* that exist in the world today, and that the rate of discovery of new species would be declining, but examination of available figures does not lend much support to this hope. For example, when Edwards (1932) catalogued the mosquitoes of the world he recognized 158 full species of *Anopheles*. Twenty-seven years later Stone et al. (1959) recognized 308 species, an increase of 95% over Edwards, and an average of 5.5 new species per annum. In other words, the number of known species has doubled in ca. 30 years. But in the subsequent 10 years since 1959 (1959–1969) about 40 additional species have been described (Stone 1967; Reid 1968, p. 45), giving an average of nearly 4.5 new species per annum. This, plus the possibility that there are more species-groups like that of *gambiae*, which are unlikely to be discovered

²G. Frizzi, U. Bianchi, and M. Mameli, 1968. Cytogenetics, biochemistry and cytochemistry as applied to microtaxonomy of *Anopheles*. An unpublished paper read in abstract at 8th International Congresses of Tropical Medicine and Malaria, Teheran.

without crossing experiments, makes it impossible to estimate how many species are still undetected.

It is interesting that comparable figures for a small part of S. E. Asia (Malaya and Borneo) agree quite well with those for the world. Gater (1935) recognized some 35 species in those 2 countries, and 33 years later Reid (1968) recognized 67, an increase of 91% over Gater. But in Africa south of the Sahara the increase in 30 years has been smaller, 68%, from 60 species (Evans 1938) to 101 (Gillies and De Meillon 1968). This may mean that there is a higher proportion of species still to be discovered in Africa, or that S. E. Asia is richer in species in proportion to its land area than is Africa. Probably the latter is the more important factor, because S.E. Asia, with its broken land mass and evergreen and monsoon rain forests, is generally considered by zoologists and botanists to be one of the world's major areas of speciation.

Returning to the question of species awaiting recognition, most systematists could point to species, or groups of species, in their area which need further analysis. For example, the *A. hyrcanus* group, to which the *coustani* group of Africa is closely related, has an enormous range from the western Mediterranean to Korea and Japan, and through S.E. Asia as far east as the Moluccas. But only in S.E. Asia and Japan have the species of the group been reasonably well described. In Malaya alone the group consists of 8 distinct species, and some of these range widely through the oriental region and show much geographic variation. The analysis of this group in other parts of its range will depend upon patient study to recognize which differences are specific and which are due to geographic variation, and will require correlating these findings with those of S.E. Asia and Japan.

Within S.E. Asia the important *minimus* group needs further study; the extent of variation in *varuna* Iyengar, which closely resembles *minimus* Theobald, is not clear, and there are other difficulties of identification in this group (Scanlon et al. 1968). These may be due to unrecognized species, but also seem to be due in part to geographic and other variations that have not yet been sufficiently described and mapped. Then there are the S.E. Asian species in the

Pyretophorus series to which the African *gambiae* group belongs. *A. sundaicus* (Rodenwaldt) is a coastal vector species, with speckled legs, that looks very like "*gambiae*". Davidson (in Soerono et al. 1965) showed that *sundaicus* from the north and south coasts of Java are fertile when crossed and thus presumably conspecific, though their larval breeding places are somewhat different. But fresh-water populations of *sundaicus* are known from considerable altitudes in the interior of Sumatra, and it would be interesting to cross this inland form with the ordinary coastal form. The latter should be crossed also with the closely similar *A. litoralis* King of the Philippines, which has recently been found carrying malaria in Sulu (Catangui et al. 1969).

Closely related to *sundaicus*, but without speckled legs, though almost indistinguishable in the larval and pupal stages, is *A. subpictus* Grassi. This is now known to be at least 2 species, *subpictus* and *indefinitus* (Ludlow) (Reid 1966). Both occur in Malaya and Java in which countries *subpictus* is confined to brackish water and *indefinitus* to fresh water. In West Pakistan, and probably most of India, only *subpictus* is known, and it occurs in both fresh and brackish water. In the Philippines only *indefinitus* is known; it is found there also in both fresh and brackish water. However, in the Philippines 3 types of egg have been described (Urbino 1936) and 3 in Java (Walch and Walch-Sorgdrager 1936). In view of this and the fact that *subpictus* is a minor vector of malaria in parts of its range (Table 1), further investigation is needed. One of the first things to do would be to map the distribution of *subpictus* and *indefinitus* and the extent of their overlap, neither of which is yet known with any accuracy. The same information is urgently needed for many other sibling species in S.E. Asia, because until their distributions are known we cannot get far with studies of their infraspecific variation, much of which is geographic.

In the detection of new species there is a great practical need to find morphological characters other than those in the chromosomes, by which individual species, particularly females, can be identified by field entomologists, so that studies of the ecology and behavior of these sibling species can be speeded up.

Table 1.—Geographic variation in vector status of some *Anopheles* of Southeast Asia.

Species	Vector in:	Not a vector (or of lesser importance)* in:
<i>aconitus</i> Dönitz	Java	India, Malaya, Thailand*
<i>balabacensis</i>	Assam to Vietnam, northern Borneo	Malaya, Philippines
<i>campestris</i> Reid	Malaya	Thailand
<i>lesteri</i>	China	Malaya,* Borneo,* Philippines
<i>leucosphyrus</i>	Southern Borneo, Sumatra?	Malaya
<i>maculatus</i>	Malaya, Sumatra and Java?	West Pakistan to Borneo and Philippines
<i>minimus</i>	Assam to Vietnam	Ceylon, Indonesia, Philippines*
<i>philippinensis</i> Ludlow	Lower Bengal to Burma	Thailand to Philippines, Malaya, Borneo, Indonesia
<i>subpictus</i>	Java, Timor, Celebes	India to Malaya
<i>sundaicus</i>	Java	Bengal*, Malaya*, Borneo*

* *A. lesteri paraliae*.

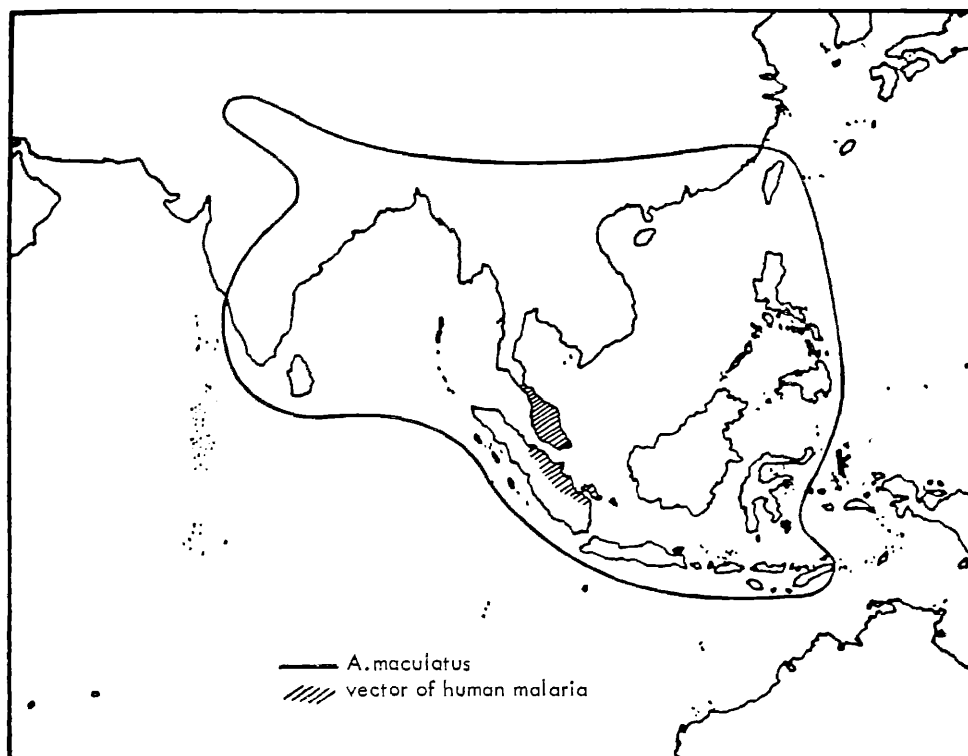


FIG. 1.—Map showing the range (bounded by the solid line) of *A. maculatus* and the area (shaded) within which it is a vector of human malaria.

The possibility of using the scanning electron microscope to look for new characters and to re-examine familiar but very small characters, like the male phallosome leaflets or the female cibarial (pharyngeal) teeth, should be considered. Study of anopheline eggs by this means by Hinton (1967) shows the sort of results that can be expected. Differences difficult to appreciate with the ordinary microscope are shown clearly and in great focal depth and may then be recognizable with the ordinary microscope.

Intraspecific Variation and Vector Status.—One thing which has emerged clearly from a study of the anophelines of S.E. Asia (Reid 1968) is that all wide-ranging species vary geographically, even if only in such characters as the number of branches on some larval hairs or the average width of the pale bands on the female palps. However, quite often this geographic variation is enough to require modifications to keys for identifying the same species in different parts of the region. When we remember that all the malaria vectors with a wide range in the region also show geographic differences in their importance as vectors (Table 1), we have a clear hint that it is time to pay more attention to geographic and other forms of morphological variation within species.

Four of the species in Table 1 are discussed in more detail here, but for lack of space and because our knowledge is incomplete, only broad outlines of

their distribution in relation to their vector status can be given.

A. maculatus Theobald (Fig. 1) has a wide range from West Pakistan (Swat) eastward to Taiwan and the Philippines and south through Malaya and Indonesia to Timor and Celebes. Morphologically, adults of *maculatus* vary considerably in a complex way. In parts of India adults show what appears to be a definite polymorphism (Reid et al. 1966); that is, 2 color forms with few intermediates are found in some areas and no associated differences have been seen in the early stages. *A. maculatus* is of little or no importance as a vector of human malaria throughout its wide range except in Malaya, where it is the principal vector in all cleared hilly land. For many years malaria control in what was then British Borneo was aimed at *maculatus* on the assumption that it was the main vector there as in Malaya. This situation remained unchanged until McArthur (1947) and Colless (1956) showed that the vector was a member of the *leucosphyrus* group and that *maculatus* in Borneo had little or no contact with man. There is substantial evidence, reviewed by Reid (1968), from comparative trapping with men and animals and from precipitin tests, that *maculatus* is a vector in Malaya, because it is much more attracted to man in that country than in Borneo and the monsoon countries to the north of Malaya. Nevertheless, despite their variability, there are no obvious differences be-

tween the adults of *maculatus* from Malaya and Borneo, and the only hint so far of a morphological difference correlated with vector status is that Malayan larvae have shorter inner sutural head hairs than those of Borneo and elsewhere.

A. minimus ranges from the west coast of India and in Ceylon eastward to Taiwan and the Philippines and south through Indonesia as far as the Celebes, but it is missing from almost all of Malaya and Borneo, where the climate appears to be too equatorial to suit it. It is an important vector of human malaria from Assam to Taiwan and the Philippines, but not in Ceylon or Indonesia. As is well known, in the Philippines, *minimus* occurs in the form *flavirostris* (Ludlow), which has a yellowish mark toward the apex of the female proboscis. This Philippine form is less man-adapted and a less potent vector of malaria than the type form with the proboscis all dark, which predominates in the monsoon countries of mainland Asia from Assam to Vietnam. But specimens with a yellow mark on the proboscis, thus resembling the Philippine form in this respect, occur sporadically throughout much of the range of *minimus*, and one wonders whether such specimens might also resemble the Philippine form in being less attracted to man than the typical form with which they occur.

A. sundaicus is found on coasts from southeast India through the archipelago to Borneo and south

Celebes, but not in Ceylon or the Philippines. A fresh-water inland form is found in a few localities in Sumatra and Java, as mentioned earlier. This species is a most important vector around the coasts of Java, but is usually of lesser or more sporadic importance and less man-adapted elsewhere. The wing is paler, with shorter dark marks on the costa, in specimens from Borneo than in those from Java and Malaya (Colless 1948).

A. balabacensis Baisas is the most widespread member of the *leucosphyrus* species group. This group contains the chief vectors of monkey malaria in the forests of S.E. Asia and is related to the *punctulatus* group of New Guinea. With a few gaps (Fig. 2) *balabacensis* ranges from the west coast of India to Taiwan and the Philippines and extends south into Malaya and northern Borneo. It is known also from western Java, but not for certain from Sumatra. It is a vector of human malaria from Assam eastward to Thailand and Vietnam, and in northern Borneo, but it is not a vector in most of the Philippines or Malaya, where distinct subspecies occur. In most of Malaya, except the extreme northwest, it occurs as subspecies *balabacensis introlatus* Colless together with *leucosphyrus* Dönitz which like it, is not a vector of human malaria there. But in Borneo, where both species are vectors, they are geographically separated, with *balabacensis* replaced by *leucosphyrus* south of a line through the north of Sarawak.

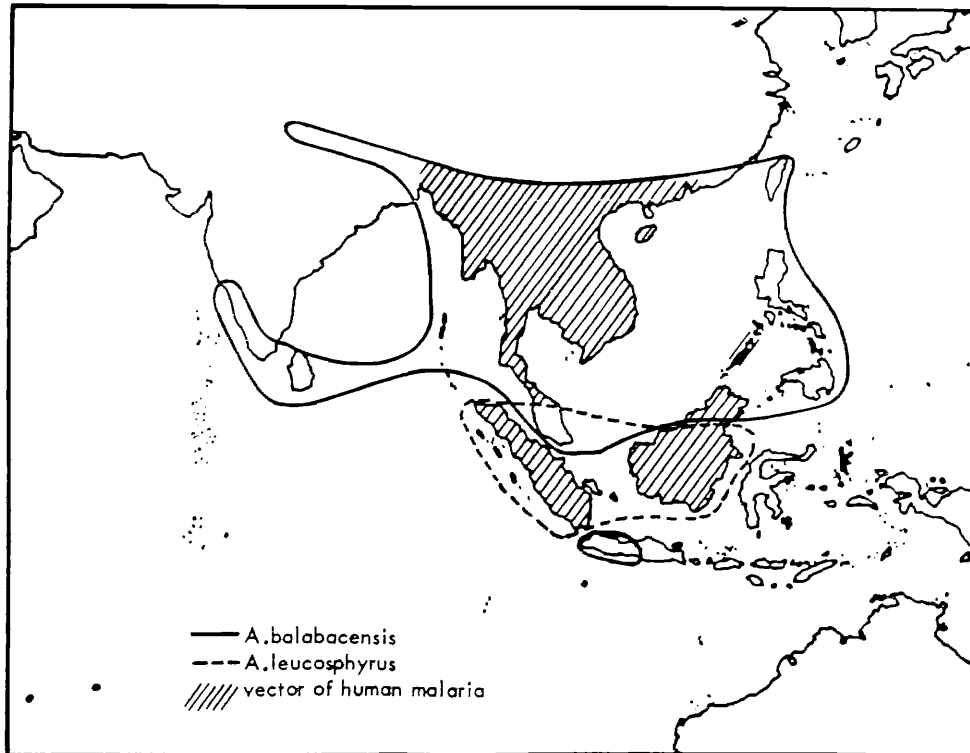


FIG. 2.—Map showing the ranges of *Anopheles balabacensis* and *A. leucosphyrus* and the areas (shaded) within which they are vectors of human malaria. Note that their ranges only overlap in Malaya where neither is a vector of human malaria.

DISCUSSION

The examples of associated geographic variations in morphology and vector status just given will serve as the starting point for a discussion of some theoretical possibilities for future advances in malaria control.

Broadly speaking, there are 2 kinds of geographic variation in morphology, the continuous or gradual and the discontinuous or abrupt. In the gradual or clinal type the characters change more or less continuously as one passes from west to east, or whatever the direction may be. Possible examples are the higher proportion of paler-winged specimens of *sundaci* in Borneo than in Malaya and Java, and the generally broader apical pale band on the female palps of *subpictus* in Malaya than in India.

In the abrupt type the characters change sharply within a short distance, and nearly all the specimens on one side of the boundary are of one form and nearly all those on the other side are of the contrasting form, and there is only a narrow zone of hybridization where both forms and intermediates between them occur. This is the classical subspecies situation in which formal subspecific names may be justified. For example, Scanlon et al. (1967) have shown that near the border between Thailand and Malaya there appears to be a narrow zone of hybridization between the vector *b. balabacensis* and its nonvector subspecies *b. introlatus*. North of this zone only the vector type form occurs, with a pale band on the base of the 4th hind-tarsal segment and no accessory sector pale spot on the costa of the wing. South of this zone only the nonvector subspecies *b. introlatus* is found, nearly all the specimens of which have an accessory sector pale spot on the costa but lack a basal pale band on hind tarsus 4. There are comparable differences between the nonvector forms of *balabacensis* in the main Philippine islands and the vector type form of Palawan and northern Borneo.

Thus in *A. balabacensis* there seems to be a close connection between morphological characters and vector status for human malaria, both of which show abrupt and correlated geographic changes. Other possible examples might be *minimus* and *minimus flavirostris*, or *lesteri* Baisas and Hu and *lesteri paraliae* Sandosham (Table 1). There seems no reason why a similar correlation between morphology and vector status should not exist also in species which show gradual or clinal changes in morphology. If so, within such species, unlike those showing abrupt geographic change in which the different forms are allopatric, there could be varying proportions of vector and nonvector genotypes occurring together in different areas, the proportions depending upon the position of each area on the cline, and these sympatric genotypes could be morphologically distinguishable. This seems to open up the possibility of malaria control in some instances by intraspecific sanitation, a refinement of Watson's earlier concept of species sanitation.

No doubt the realities will prove to be much less simple than this, but there does seem to be a case for looking very closely at variation in species such as *maculatus*, *sundaicus*, or *subpictus*. Their variations would need to be studied and mapped, as would those of *minimus*, which may well prove to show both clinal and abrupt geographic change. The relative abundance of any distinct variants in different areas should be established. Then field and laboratory studies should be made of such factors as their degree of attractiveness to man vs. animals, susceptibility to malaria parasites, adult and larval habits and their genetics, with the ultimate aim of finding means to reduce or eliminate those variants with the greatest potential as vectors of human malaria.

At first sight this may seem a rather impractical objective, but we should remember that there is no lack of other evidence to show that in mosquitoes sympatric infraspecific variations occur that are likely to affect vector status. Some of the variants may have sufficiently distinct adult or larval habits to offer a target for selective control measures. For example, in *Aedes aegypti* (L.) on the Kenya coast the indoor, more man-adapted, pale variety *queenslandensis* Theobald occurs alongside the more outdoor, less man-adapted, and darker type form (McClelland 1960); within the *Culex pipiens* complex are both man-biting and nonman-biting forms (Matingly 1967); and it is a fact that anopheline host preference (Gillies 1964) and susceptibility to parasites (Macdonald 1967) are genetically controlled and can be selected. Finally, we know that chromosomal polymorphism is common in *Anopheles*, and that similar polymorphisms in *Drosophila* are adaptive and vary in their proportions in the species populations, not only geographically, but also locally with the seasons or over longer periods (Dobzhansky 1961). If the same applies to *Anopheles*, such changes in the proportions of different chromosomal polymorphisms could sometimes be a factor in those occasional puzzling fluctuations in local malaria transmission that do not seem to be accounted for by the more usual and obvious factors, such as changes in the numbers of the vector or of gametocyte carriers. If this were so, it might be possible, given sufficient knowledge, to manipulate the environment so as to favor those polymorphisms with the least vector potential.

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