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Occurrence and Distribution of the *Culex pipiens* Complex*

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Culex pipiens *is the most widely distributed species of mosquito in the world, the typical form being found in temperate regions and the subspecies,* fatigans, *in the tropics.* Fatigans *is morphologically and biologically uniform in different geographical regions, whereas* C. p. pipiens *is very variable. Where the two forms come into contact, hybrid swarms occur. The only clear distinction between the two forms is in the nature of the male genitalia.*

Molestus *should not be considered to be distinct from* pipiens*; the only good criterion for the taxonomic recognition of* molestus *is that it is autogenous.*

The ancestral form is probably pipiens, *which arose from a stem from the Ethiopian region. It probably colonized the northern temperate region fairly slowly, giving much variation between populations.* Fatigans *appears to have arisen from southern* pipiens *populations.* Molestus *seems to be an ecological race of* pipiens *which develops wherever the proper selective influence acts.*

Any review of this complex of mosquitos must necessarily be strongly biassed by the interpretations of the reviewer. Although I shall try to be as objective as possible in my treatment of the group, it must be understood that my interpretation may not be shared by others.

If *fatigans* is a subspecies of *Culex pipiens*, as most recent workers indicate, then *pipiens* is the most widely distributed species of mosquito in the world, the subspecies *fatigans* being found throughout the tropics and the typical subspecies *pipiens* throughout temperate regions, except in the coldest climates. The only clear-cut distinction between the two forms is in the nature of the male genitalia; eggs, larvae, pupae, and females have not been reliably differentiated.

The subspecies *fatigans* (I use this name in deference to European workers, although *quinquefasciatus* appears to be the correct one) is found throughout the tropics and is fairly uniform in appearance and in biological characteristics wherever found. It is characteristically found in water heavily charged with organic matter, either in ground pools or in containers of various types. It may be found in rather clean water on occasion, but tends to be replaced by related species in such habitats. Blood, or in the laboratory other proteinaceous materials, is required for the maturation of eggs; there is no well-documented exception to this. When one studies autogenous *pipiens* one realizes that autogeny of this type would be quickly found in *fatigans* if it were present. The enormous amount of work that has been done on so many different strains of *fatigans* clearly shows that autogeny of the *pipiens* type occurs very rarely, if at all, in *fatigans*. Laboratory colonies of *fatigans* are usually initiated with ease, even in rather small containers.

C. p. pipiens, on the other hand, is a very variable form, both morphologically and biologically. It is, in general, found throughout temperate areas of the world, except in extremely cold areas. The most northerly situation of this subspecies to about 45°N in the New World and about 63°N in the Old World. In the southern hemisphere it is found in South Africa, South Australia, and, according to Dyar (1928), in South America south of latitude 39°S. The ranges of *pipiens* and *fatigans* meet in various parts of the world—in North America, South America, East and South Africa, in the Near and

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Far East, and in Australia. In these places forms intermediate between the two subspecies are customarily found, and these are frequently called *pallens*. Such populations have been studied intensively in North America and the Far East and all indications are that they are hybrids. The name *pallens* therefore should not be used except in a vernacular sense.

The distributions of *pipiens* and *fatigans* suggest that temperature is of prime importance as a limiting factor. *Pipiens* is well adapted to temperate climates, which cannot be tolerated by *fatigans*, apparently because of its inability to cope with low temperatures. There is no obvious reason for the absence of *pipiens* from tropical regions. Perhaps this is due to deleterious effects of high temperature or to undetected competition from *fatigans*. An interesting confirmation of the importance of temperature in the distribution of these subspecies has recently been discovered in California. The Central Valley of California is an elongated basin which runs in a north–south direction for about 450 miles (ca 720 km). Cool air enters this basin through a gap in the mountains near the middle. Part of the air then moves north and part south. Insolation of the valley warms the air as it moves either north or south. For this reason the coolest part of the valley is in the middle; the highest temperatures are usually recorded in the extreme south and north. Some agricultural crops reflect this irregularity; oranges, for example, are grown at the warm ends of the valley but not in the cooler central part. Almost pure populations of *Culex pipiens* are found in the centre of the valley but these merge with *fatigans* at the ends. In this case nature has provided a reversed temperature gradient and the *pipiens* complex responds with a reversed *pipiens–fatigans* cline.

The chief difficulty with *pipiens* is the problem of autogeny. Marshall & Staley (1937) described a series of morphological differences between autogenous (which they called *molestus*) and anautogenous *pipiens*. Studies by these workers, Tate & Vincent (1936), Roubaud (1933) and his associates, and others indicated that the autogenous form mated in small spaces, attacked man readily, and did not diapause during the winter. The anautogenous form required a large space in which to mate, attacked man rarely or not at all, and diapaused during the winter. These morphological and biological differences suggested that autogenous and anautogenous *pipiens* were different species.

There is no doubt about the reality of the morphological differences described by Marshall & Staley (1937). There is serious doubt, however, whether their morphological characterization of "*molestus*" is true of other autogenous strains. There is also serious doubt whether the biological characterizations of these strains is correct. Unfortunately, most of the work on these forms was done on laboratory strains that had previously undergone selection.

It now appears that the only invariant characteristic of strains of "*molestus*" is that they are autogenous, and the name has come to denote only that. Furthermore, autogeny has now been shown to be controlled by a relatively few genetic factors. There is a need to study natural populations to determine the frequency of autogeny in such populations. Spielman (1961) has reported the mixture of autogenous and anautogenous forms in nature in Boston.[1] Knight & Abdel-Malek (1951) studied "*molestus*" populations in Egypt and found that only 1% of the females were autogenous. It seems likely that the entire concept of autogenous and anautogenous populations as distinct biological entities in nature is largely a figment of the imagination. There are undoubtedly populations in relatively isolated subterranean habitats in which selection for autogeny is very strong. There undoubtedly are also populations that conform fairly closely to the classic concept of anautogenous eurygamous, ornithophilous, non-hibernatory strains. There is an urgent need, however, to determine whether all or most natural populations tend to fall into one or other of these extreme types or whether, as is more likely, genes for autogeny are found at a low level in most populations of *pipiens* and can serve for selection of autogenous strains when the proper environmental conditions ensue. The work of Laven (1957, 1959)[2] on intersterility of autogenous strains certainly suggests that such strains may not have a common origin but may be independently derived from the parental form, typical *pipiens*. Conflicting studies on the inheritance of autogeny also suggest that autogeny may rest on different genetic bases in different populations. It seems likely that autogeny is a characteristic that is selectively advantageous in certain ecological situations and that this phenotype tends to be selected for whenever *pipiens* invades such habitats.

Finally, I should like to summarize my present opinion as to the evolution of this group. *Culex*

[1] See also the paper on page 271 of this issue.

[2] See also the paper on page 263 of this issue.

species that are fairly closely related to *pipiens* tend to be eurygamous and ornithophilous, to breed in relatively clean ground pools, and to diapause. Typical *pipiens* therefore seems to be, from a biological point of view, a fairly typical member of the subgenus *Culex*. *Fatigans*, on the other hand, has a whole complex of biological characteristics unusual for this subgenus: stenogamy, anthrophily, domesticity, container-breeding, breeding in foul water, and a poorly developed diapause. The male terminalia, in my opinion, also show a greater degree of development than do those of *pipiens*. The evidence therefore indicates that *pipiens* is ancestral to *fatigans*.

Ross (1953) considers the *pipiens* group to be derived from the *guiarti* group, which is presently found chiefly in Ethiopia. It seems likely that an ancestral form no longer present arose in tropical Africa and invaded the northern temperate region of the world; typical *pipiens* then differentiated at some place in the northern temperate region and subsequently spread slowly over the whole of the temperate region. This species bred in ground pools of clean water, was ornithophilous and eurygamous, and was capable of hibernating by undergoing an ovarian diapause in response to shortened day-length.

At some place near the southern edge of the range of *pipiens* a new form, *fatigans*, developed that differed in having greater enlargement of the male terminalia. This form bred in foul water in ground pools or containers, mated in small spaces, and lost its ability to withstand a high degree of cold. By breeding in foul water it was able to utilize a habitat that was not effectively used by its close relatives. It spread over the whole of the tropics, possibly in association with man. *Fatigans* breeds chiefly in water fouled by man, in ground pools and containers around human habitations and his livestock. It readily enters and rests in human dwellings and in the process feeds on man. It can therefore be considered a domesticated species and is eminently susceptible to transportation by man. The morphological and biological uniformity of *fatigans* throughout the tropics certainly suggests a high degree of mobility and rapid colonization.

The expansion of the range of *fatigans* has brought it into contact with *pipiens* populations in many areas where the northern temperate region verges on the tropics, in the Near and Far East, and in North America. In these areas hybridization occurs, which gives rise to populations known as " *pallens* ".

The biological characteristics of *fatigans*, however, are not peculiar to that form. All are found in various populations of *pipiens*. Therefore it is easy to see how a subterranean habitat, such as a septic tank, would select for autogeny, stenogamy, and tolerance of foul water. Once such a strain developed, it could be transported as easily as *fatigans*. That this has occurred is demonstrated by the finding of a hybrid swarm at Malibu Beach in Southern California (McMillan, 1958). This population is surrounded by populations of *fatigans* but retains its hybrid character, as judged by details of the male terminalia. It also continues to be autogenous, which clearly shows that it arose by introduction of autogenous *pipiens*, which are commonly found on the coast a hundred or so miles further north.

Populations of *pipiens* in the southern hemisphere have not received the study they deserve. The form in Australia has been shown to be autogenous and presumably is introduced. Galindo (1939) deduced that the form found in Argentina and possibly Chile is autogenous. Edwards (1941) indicated that the usual form found in the Ethiopian region is anautogenous, but Mattingly (1951) mentioned records of autogeny from the Sudan and the Congo. It would thus appear that forms found in the southern hemisphere are autogenous and introduced, except possibly in the Ethiopian region.

RÉSUMÉ

Culex pipiens est l'espèce de moustique la plus répandue à travers le monde, si l'on admet que *fatigans* en est une sous-espèce. Ce dernier (que l'on devrait plus correctement nommer *quinquefasciatus*) se rencontre sous les tropiques; ses caractéristiques morphologiques et biologiques sont relativement constantes. Il vit surtout dans les eaux fortement polluées et la maturation des œufs exige la prise d'un repas de sang. *C. p. pipiens*, qui vit dans toutes les zones tempérées du monde, a des caractères morphologiques et biologiques très variables. La seule différence nette entre les deux sous-espèces réside en la conformation des organes génitaux mâles.

Dans diverses régions, les deux espèces cohabitent et l'on trouve alors des formes intermédiaires que l'on appelle fréquemment *pallens*. La température ambiante semble être le facteur limitant la zone dans laquelle peut

vivre l'une ou l'autre sous-espèce; alors que *pipiens* supporte bien le climat tempéré, *fatigans* ne peut s'adapter aux basses températures.

L'autogénie est le seul caractère que l'on peut considérer comme invariable des souches de *molestus*. Ce caractère qui dépend d'un petit nombre de facteurs génétiques est favorisé par certaines conditions écologiques.

Selon l'auteur, les espèces de *Culex* proches de *pipiens* tendent à l'eurygamie, à l'ornithophilie, à la diapause et à la recherche d'eaux relativement propres. *Fatigans* a des caractères inhabituels au sous-genre *Culex*: sténogamie, anthropophilie, recherche des habitations, faible diapause; il installe volontiers ses gîtes en eaux croupissantes. Les organes génitaux mâles sont plus développés que ceux de *pipiens*. *Fatigans* serait le descendant de *pipiens* qui dériverait lui-même du groupe *guiarti* trouvé à l'heure actuelle surtout en Ethiopie. *Pipiens* se serait ainsi lentement répandu dans les régions tropicales septentrionales tandis qu'à la limite méridionale de sa zone de peuplement se développait la forme *fatigans* dont la distribution indique une grande mobilité et une forte capacité de colonisation. Cette expansion a favorisé l'hybridation entre *pipiens* et *fatigans* donnant ainsi naissance aux populations dénommées *pallens*.

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