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# THE SYSTEMATICS OF THE CULEX PIPIENS COMPLEX[1]

by

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## The Culex pipiens complex as a polytypic species

The systematics of the Culex pipiens complex, as a whole, were last reviewed 13 years ago (Mattingly et al., 1951). The main conclusion reached was that the members of the complex then recognized (C. p. pipiens Linnaeus, C. p. fatigans Wiedemann, C. p. var. molestus Forskal, C. p. var. pallens Coquillett, C. p. var. comitatus Dyar & Knab) could most usefully be treated as a single polytypic species. Mayr (1963) accepts this conclusion. I am in complete agreement with him. In my opinion the considerable body of evidence which has accumulated in the interim merely strengthens this view. In the New World, Barr (1957, 1960) has shown that morphologically intermediate forms are widely distributed in North America. In the Old World, Bekku (1956) has shown that there is continuous variation in Japan, as between C. p. pipiens in the north and C. p. fatigans in the south, and Rioux & Pech (1959) have summarized the evidence for the occurrence of various combinations of autogeny, anautogeny, stenogamy, eurygamy, anthropophily, ornithophily and homo- and hetero-dynamy in Southern France and North Africa. Similar evidence has been found in Italy (La Face, 1957, 1961; Rossi-Espagnet, 1957). Evidence of reproductive continuity between C. p. pipiens and C. p. var. molestus in North America was noted in the 1951 symposium. Ikuzawa (1955) records morphological intergradation between C. p. var. pallens and C. p. var. molestus in Japan. Finally, Vinogradova (1961) has concluded from a study of the inheritance of adult diapause in C. p. pipiens and C. p. var. molestus hybrids that hybridization can take place and that the establishment of hybrids will depend on the extent to which their seasonal cycle is adapted to local conditions. Other crossing experiments have continued to imply genetic continuity between North American C. p. pipiens and C. p. fatigans and between the latter and C. p. var. molestus (see, for example, Dobrotworsky, 1955; Kitzmiller & Laven, 1954; Knight, 1953; Rozeboom, 1958). Pal & Krishnamurthy (1958) failed with crosses between C. p. fatigans and C. p. var. molestus. The reasons for this are obscure. Parker & Rozeboom (1960) showed that molestus is at least as sexually active as fatigans at high temperature, providing further evidence of the much closer resemblance between these two forms than between either of them and C. p. pipiens.

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However, Tekle (1960) has shown that there is a wide temperature range over which larvae of both C. p. pipiens and C. p. fatigans can complete their development, and attempts to elucidate barriers to interbreeding which might operate in temperate and subtemperate latitudes have met with little success (Rozeboom & Gifford, 1954; Parker & Rozeboom, 1960; and see below).

In view of this accumulation of evidence it may seem surprising that Stone (1963), in his second supplement to the Synoptic catalog of the mosquitos of the world (Stone, Knight & Starcke, 1959), has raised both C. p. ssp. fatigans and C. p. ssp. australicus (for which see below) to specific rank. The explanation is that Stone has followed Belkin's monograph of the mosquitos of the South Pacific (Belkin, 1962). In this book, however, Belkin specifically disclaims any attempt at infraspecific analysis and excludes all infraspecific names. This cannot be said to amount to a critical revision of the present complex. To be consistent, Stone should have excluded all infraspecific names from the catalogue. The latter is a most valuable and authoritative work and it is to be hoped that the matter will be attended to in the next supplement.

## Infraspecific taxonomy of the complex

Since the publication of the 1951 review (Mattingly et al., 1951), two further members of the complex have been discovered. These are C. pipiens ssp. australicus Dobrotworsky & Drummond (1953) and C. globocoxitus Dobrotworsky (1953). With this exception the nomenclature proposed in 1951 appears still to provide an adequate framework within which to develop our ideas. Rioux & Pech (1959) have proposed the use of four varietal names to distinguish different combinations of the biological characters noted above as occurring in southern Europe and the Mediterranean area generally. Such a treatment, if extended to other possible combinations of these characters, would lead to an excessive multiplication of names. Moreover, there also exist varietal names based on morphological characters (sternopallidus and sternopunctatus Roubaud). It is thus quite possible for the same form to be known under two different varietal names, one deriving from its biological and the other from its morphological characters. It is precisely this type of abuse of the varietal category which has led to its abandonment by many taxonomists (see, for example, Mayr, 1942). At the present time it is customary for English-speaking geneticists and others, interested in autogeny, to speak of C. p. var. molestus while public health officials, concerned with man-biting C. pipiens in cities, use the same name for these forms. This does no harm and causes no confusion. If French workers prefer the name var. autogenicus, as more familiar, they are at liberty to use it but such names should not be multiplied beyond what is absolutely necessary. It should also be noted that such names are not subject to the rule of priority (though it is customary among mosquito workers to follow this rule as far as possible). Finally, they should not be used in such a way as to give an impression of precision which they cannot, by their very nature, possess. (It may be noted, for example, that Laven (1954) has produced evidence for multiple allelism of one of the genes involved in autogeny.)

The populations of C. p. var. molestus shown by Laven (1959 etc.), and by Dobrotworsky (1955) in Australia, to be largely or wholly reproductively isolated, by cytoplasmic factors, pose a more serious and fundamental problem. Laven suggests that the phenomena encountered may imply the occurrence of "a kind of speciation perhaps common in mosquitos". This is possible, but sterility barriers in Aedes (for which see references in Mattingly (1956) and also Woodhill (1959), McClelland (1961), Mattingly (1964)) and Anopheles (discussion and references in Bates (1949) and see Davidson & Mason (1963)) involve various phenomena including both maternal and paternal inheritance, blending inheritance and sterility of $F_1$ offspring of either or both sexes as well as larval and embryonic mortality. Even within Laven's crosses a variety of phenomena has been observed, ranging from complete sterility through the production of females of parthenogenetic origin to the production of small numbers of normal offspring. It seems that there is a growing need for an interpretative review of the increasingly complex picture presented by sterility in mosquito crosses.

Laven (1959) has argued that the occurrence of a cytoplasmic factor of this kind would permit speciation within a sympatric population. On the basis of a mathematical analysis by Caspari & Watson (1959), Mayr (1963) has argued that two different kinds of cytoplasm can only become established allopatrically since either the new or the old cytoplasm will be eliminated from any population in which the change arises. He therefore concludes that cytoplasmic factors of this kind can act only to reinforce other factors involved in allopatric speciation. This does not fully answer Laven's case, but the matter cannot be further discussed here. Mayr finally concludes that ". . . there is serious doubt whether it would be legitimate to label as 'species' allopatric strains that may differ by only a single factor". This point also will probably be argued, but certainly I would think that most systematists would be better satisfied if there were more evidence regarding the nature of Laven's factors, their effect on the adaptiveness of the genome and their stability under varying environmental conditions. Even more important from the point of view of the systematist, and therefore of the present paper, is the question of whether there yet exists sufficient evidence of de facto interruption of gene flow between the populations cited by Laven (1959). Two of these, originally thought to be reproductively isolated, namely the South German and West European, have since been shown to be linked, at least potentially, by a third population, from Österberg in southern Germany, which is fully compatible with both. It would seem to be premature to assume that similar annectent populations will not be discovered elsewhere. A comparative morphological study of allegedly isolated populations also seems very desirable. Spielman (1957), by his analysis of the genetic basis of autogeny, has provided the population geneticist with a valuable tool. The same author (1964) has used this in a study of sympatric populations of autogenous and anautogenous C. pipiens in the United States. It would be premature to comment on his results until they are fully published. However, my own experience of C. p. var. molestus as a public health problem in Great Britain would suggest that periodic outbreaks of this mosquito might be associated with facultative eurygamy and hence with possibilities for hybridization with C. p. pipiens. These would be expected to occur with increasing frequency in lower latitudes, which would be consistent with the extensive intergrading observed in southern Europe. It is, perhaps, surprising that there are almost no records of autogeny in C. p. fatigans. As already noted, the apparent failure of C. p. var. molestus to thrive in tropical environments remains unexplained.

However, it seems clear that autogeny, as such, would have relatively little selective advantage in the tropics and subtropics. It is comparatively rare in wild populations in Egypt (Knight & Abdel Malek, 1951). Bhatnagar et al. (1958) have a record of autogeny in C. p. fatigans in India but the strain proved non-viable and so few observations were made that little comment is possible. One case of alleged autogeny which came to my notice was apparently due to egg retention in C. p. fatigans (which may last several weeks so that when rafts do appear they are thought to have been produced without a blood meal).

Among morphologically intermediate forms, C. p. australicus is particularly interesting since it apparently occurs in the complete absence of C. p. pipiens. Various explanations are possible. It has been suggested that this and C. globocoxitus may be primitive members of the complex. I would think, however, that both could have arisen from introduced populations. C. p. australicus is at present known only from Australia (Dobrotworsky & Drummond, 1953), New Caledonia (Marks & Rageau, 1957) and New Hebrides (Rageau & Vervent, 1958; Laird, 1961). C. globocoxitus is known only from southern Australia. More information regarding seasonal and geographical variation, particularly of the former, would be welcome.

As noted above, attempts to disclose mating barriers between North American members of the complex have met with only very limited success. In my view such barriers are likely to be less important in determining the character of a particular population in nature than is the relative fitness, in a particular environment, exhibited by the hybrids. Some workers on the A. gambiae complex have recently claimed to have found hybrids in nature despite the occurrence of $F_1$ male sterility. In this connexion may be mentioned the remarkable observation by Spurway (see Spurway & Asit Kumar, 1960) that intersubspecific hybrids of European newts can produce more offspring in the laboratory than their parents even in the presence of markedly abnormal spermatogenesis. A possible means of gaining some insight into the relative importance of "hybrid vigour" would be the maintenance of population cages under a variety of environmental conditions and studying the equilibria established between parent forms and hybrids. Studies of this kind have recently yielded very interesting results with A. aegypti (Coker, 1964; Adhami & Craig, in press; Hickey, in press). McMillan (1958), in an interesting study of seasonal variation in the morphological characters of wild and caged populations of different members of the pipiens complex, including intermediates, has concluded that seasonal changes in DV/D ratio in the natural population may be associated with an influx of C. p. fatigans from the south during the warm part of the year. One wonders whether increased eurygamy of C. p. fatigans at that time may not have played a part, as is suggested above in relation to C. p. var. molestus in southern Europe. It is not clear that the direct effect of temperature on DV/D ratio has been adequately studied.

It is only possible to mention in passing the obvious possibilities for wider understanding inherent in the study of cytogenetics. This study has hitherto played little part in the evolution of our ideas regarding the C. pipiens complex. Now that chromosome maps are becoming available (Kitzmiller & Keppler, 1961), many possibilities are likely to open up. (For a general review, see Kitzmiller, 1963).

Time has not permitted a review of work on morphological variation within the complex though this is extensive and interesting. Some characters such as male palp indices, siphonal index and chaetotaxy, length of anterior fork cell of wing and sternal markings have received attention. Others, known to show significant variation, such as tergal markings, number of lower mesepimeral bristles and shape of the ventral arm of the phallosome, have not. A review on these lines would be very useful.

## Limits of the *C. pipiens* complex

The record of Dobrotworsky (1953) of naturally occurring hybrids between *C. p.* var. *molestus* and *C. globocoxitus* should warn us against closing our minds to possible extensions of the complex as at present conceived. A curious problem is presented by specimens, apparently of *C. p. pipiens*, from south-west England, with an extra patch of scales on the pre-alar knob of the sternopleuron. I have seen this character nowhere else in any member of the complex. The absence of these scales normally distinguishes *C. pipiens* from *C. torrentium* Martini. The latter was formerly known only from Scandinavia and North Germany. It appears to have been introduced into Britain during the war (Mattingly, 1951) and has now become widespread and seems to be replacing *C. p. pipiens* to some extent. It also appears to have extended its range southwards and, besides being found in southern England, has been recorded from as far south in France as the eastern Pyrenees (Sicart & Ruffié, 1958). The occurrence of these scales might suggest hybridization between *C. p. pipiens* and *C. torrentium*, were it not that the latter also exhibits an additional pleural scale patch, on the post-spiracular area, in the same part of the country. This is a remarkable phenomenon and it is unfortunate that no one in that part of Britain has yet undertaken to investigate it. *C. torrentium* belongs to the *C. trifilatus* complex which, like the *C. pipiens* complex, is widespread in the Old World and shows signs of having been markedly affected by human interference.

## Summary

The last comprehensive review of this complex was published in 1951. In the ensuing 13 years, evidence has continued to accumulate which would suggest that this is a single polytypic species. Morphologically intermediate forms are widespread in parts of both the New and the Old World and experiments on temperature tolerance and mating preferences, as well as crossing experiments, have failed to reveal insuperable barriers to hybridization. Suggested amendments to nomenclature have proved to be insufficiently critical and cannot be accepted. The nature and extent of hybrid sterility is a problem of increasing importance in relation to several mosquito complexes. Some recent discussions of Laven's cytoplasmic factors are noted in this context. Systematists will probably prefer to wait for more direct evidence regarding the extent of gene flow before committing themselves. It is suggested that the relative fitness of hybrids may be more important in determining their rarity or otherwise in particular populations than the rather tenuous mating barriers so far demonstrated. The use of population cages to study the equilibria arising between parent forms and hybrids may provide the most useful tool for further exploration of the complex. Two new forms have been added to the complex since 1951. It is

suggested that it would be unwise to neglect its dynamic aspects or to regard its limits as fixed or, as yet, ascertained. Evidence suggestive of extensive replacement of C. p. pipiens by C. torrentium in England, and possibly elsewhere in western Europe, carries a similar warning with respect to the geography of the complex. A comprehensive review of the morphological aspects of the complex is badly needed.

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