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A Possible Model for Speciation by Cytoplasmic Isolation in the *Culex pipiens* Complex*

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Evidence so far available indicates that in the Culex pipiens *complex there exists a genetic system with unique properties not comparable with those of the chromosomal gene system and probably involved in a mode of speciation peculiar to this complex. In a long series of backcrosses it has been shown that probably every* Culex pipiens *population contains a factor that is inherited through the cytoplasm, the only phenotypic expression of which is the crossability or non-crossability (incompatibility) of a given strain with other strains. That there is a whole series of such cytoplasmic factors is indicated by the twenty or so crossing types of* Culex *strains found throughout the world.*

In closed populations it seems likely that, as a result of genic diversification, a modification occurs that will eventually lead to differences in traits determined by genes.

Any discussion about speciation must start with a definition of the term " species ". The one adopted here is that of Mayr (1942), which has been accepted and used in the two-and-a-half decades since its publication by most biologists, including geneticists —namely, " Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups ". Mayr concluded recently (1963), after a thorough review of the problem, that geographic speciation is the almost exclusive mode of speciation among animals. Contiguous populations are united by a genetic cohesion and the flow of newly arising mutations is uninterrupted throughout the populations. Therefore only spatial isolation of two or more parts of such population will break the flow of genes and restrict newly arising genes to the isolates. The accumulation of genetic differences of several kinds (morphological, ethological, chromosomal) will make the two or more isolates divergent to such an extent that, even after breakdown of the geographic isolation, gene flow is no longer possible.

SPECIATION BY SPATIAL ISOLATION

The basic assumption in a working hypothesis of speciation by spatial isolation is that all differentiation must be genic. Consequently, under such an assumption, diversification can come about only by a slow build-up of genetic differences. Any major mutation would lead to lowered chances of reproduction or to reproductive death of the inflicted individual. However, there is by now ample evidence that, besides the genetic system of chromosomal genes, other genetic systems exist in plants and animals. One of these, the so-called plastidom, based on independent genetic determinants in the plastids or chloroplasts, is restricted to higher plants and some unicellular organisms (flagellates). For a third system, the so-called plasmon, i.e., independent determinants in the cytoplasm, only a few unquestioned cases are known. *A priori*, it is not necessary to suppose that the determinants in the last two systems should undergo, as a whole, the same slow stepwise differentiation that occurs in the chromosomal gene system. All evidence at present available seems to indicate that, in some Culicidae, and especially in the *Culex pipiens* complex, there is a genetic system with unique properties not comparable with those of the chromosomal gene system and probably involved in a way of speciation peculiar to this complex. In a long series of back-

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crosses we have shown that probably every *Culex pipiens* population contains a factor that is inherited through the cytoplasm, the only phenotypic expression of which is the crossability or non-crossability of a given strain with other strains. Non-crossability or incompatibility, i.e., the lack of offspring in certain cross-combinations, is in itself a perfect isolating mechanism. It is more effective than most of the many isolating mechanisms based on complex genic differences. Moreover, there is not only one such cytoplasmic factor that brings about isolation between different strains; there must be a series of different ones, as evidenced by the 20 or so crossing types found over a considerable period in *Culex* strains all over the world (*Bull. Wld Hlth Org.*, 1966).

Besides the fact that these cytoplasmic incompatibility factors operate as perfect isolating mechanisms, there is also evidence that they can come into existence and function in a much simpler way than the complex genic isolation systems. There exist some 20 different cytoplasmic incompatibility factors, all operating as isolation mechanisms by determining the crossability of each type in a specific pattern. Natural variability is therefore evident, and it seems reasonable that this variability originated by a process of mutation of the determinants. Obviously, there is no change of the determinants, and therefore of the crossing type, in a stepwise way, because factors with an intermediate effect (suppression of part of the offspring) have never been observed. A " mutation " of a given cytoplasmic factor to another " type " leads to a clear-cut result (no offspring) in one single step.

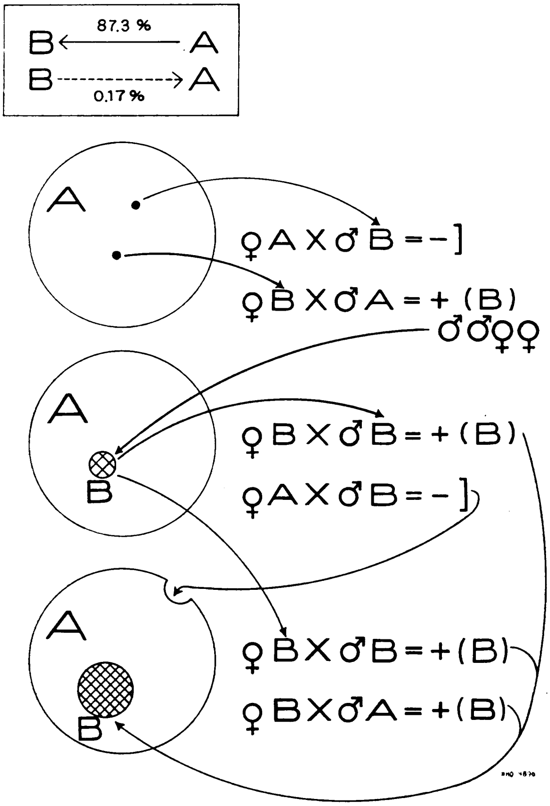
ORIGIN AND FUNCTION OF CYTOPLASMIC INCOMPATIBILITY FACTORS

The following considerations on the origin and function of different cytoplasmic incompatibility factors will serve only as a theoretical model for the origin of the diversification and " speciation " in the *Culex pipiens* complex. This model will show how, in a panmictic population of *Culex*, new species can arise without spatial isolation (geographical speciation). Whether it will be possible to substantiate this model by experiment remains to be seen. Nevertheless, the existence of cytoplasmic isolation between *Culex* populations without genic differences forces us to consider the cytoplasmic factors as determinants of speciation in the *Culex pipiens* complex.

Suppose we have a panmictic population A of *Culex*. All mosquitos in the whole distribution area are interfertile. Suppose next that a " mutation " of the cytoplasmic factor A to B (Fig. 1) occurs. The new " type " B should have the characteristic that all males of type B can no longer produce offspring with females of the original type A, but that females of the new type B are still fertile with males of type A (unilateral incompatibility). If the supposed " mutation " from A to B occurs in males, the new type will become lost as soon as it appears. But B females will have offspring with A males and will pass the factor B to the offspring, males as well as females. The offspring are, of course, interfertile and produce an ever-expanding population of type B. The B females will still produce offspring after copulation with males of the surrounding population A, but males of the new type B, mating with A females, will " kill " their offspring. The mutation of A to B therefore sets in motion a process of multiplication of type B and replacement of type A. Evidently only a single mutational event from A to B in only a

FIG. 1

EFFECT OF MUTATION OF CYTOPLASMIC FACTOR

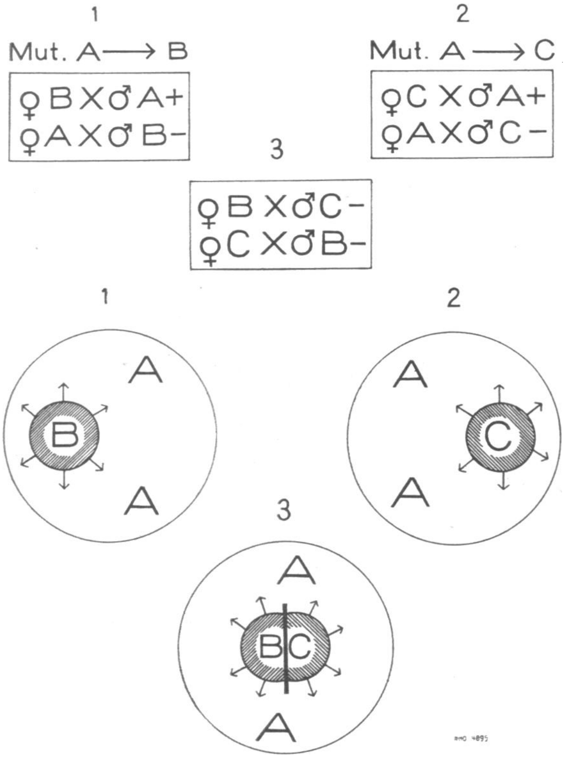


single female will be sufficient for this shift in a population. There is no necessity for any spatial isolation to occur before these events can happen because the change of type A to type B is in itself a perfect isolating mechanism. The ultimate result of such a mutation will be the replacement of type A by the new type B in the whole area of the former panmictic population A.

However, anywhere in the remaining area of type A a second mutation could occur, this time from type A to type C, with the characteristic that C females will remain compatible with A males but C males will no longer be compatible with A females (Fig. 2). Such a mutation could happen anywhere in the area of A—far apart from the point where B appeared, in close proximity to this point or in the region of overlap between type B and type A. Again, there is no correlation between the mutational event itself and the point of origin and therefore there is again no need for previous spatial isolation. As indicated by the letter C, this type is different from B in such a way that type C is incompatible in both crossing directions with type B. The two new types B and C will eventually eliminate type A or replace it to a certain extent until other factors prevent a further progression of B and C. But where B and C meet, they will produce no offspring. If type A disappears, only types B and C will remain and they can exist side by side only as two separate populations without any flow of genes from one type to the other, i.e., they are two full species.

FIG. 2

EFFECT OF SECOND MUTATION OF CYTOPLASMIC FACTOR



Such a situation—namely, the existence of two reproductively isolated populations side by side with the characteristics of type B and type C, respectively—has been found in the *Culex pipiens* complex between northern Germany and Western Europe. A population with the characteristics of type A, and therefore a possible source of types B and C, has been found in southern Germany. In spite of this correspondence between the proposed model of speciation by cytoplasmic isolation and the observation of natural populations with the same characteristics, I am not yet prepared to declare that *Culex* from northern Germany and *Culex* from Western Europe belong to two different species. There is an urgent need for an investigation of the populations between the different geographical points of observation. It is at present impossible to predict the outcome of such an investigation.

CONSEQUENCES IN CLOSED POPULATIONS

Finally, it seems likely that in closed populations, such as B and C, in addition to the previous cytoplasmic diversification and isolation and also as a consequence of genic diversification, a modification may occur that would eventually lead to differences in traits determined by genes. Geographical differences, e.g., in insecticide-resistance or other traits of importance in vector control, may find an explanation in the existence of such closed populations. Their existence can only be shown by test-crossing.

RÉSUMÉ

Dans ce travail, on adopte la définition de l'espèce donnée par Mayr en 1942. D'après les études faites jusqu'ici, le complexe *Culex pipiens* posséderait un système génétique dont les propriétés particulières ne sont pas

comparables au système génétique chromosomique. La manière propre dont se forment les espèces dans ce groupe serait probablement due à ce système. L'auteur, grâce à de nombreux rétrocroisements, a pu montrer que chaque population de *Culex pipiens* contient un facteur transmis par le cytoplasme dont la seule expression phénotypique est la compatibilité ou l'incompatibilité avec d'autres souches. L'absence de descendance dans les cas d'incompatibilité est déjà, par elle-même, un mécanisme d'isolement parfaitement efficace. Un tel facteur cytoplasmique n'est pas le seul, il y en a probablement une vingtaine qui agissent tous comme des mécanismes d'isolement par la détermination des possibilités de croisement.

L'auteur construit un modèle théorique de l'origine des différenciations et de la formation des espèces dans le groupe *Culex pipiens*. Considérant seulement l'origine et la fonction de différents facteurs cytoplasmiques, il tente de démontrer comment de nouvelles espèces peuvent se former sans isolement spatial. Il semble enfin que dans des populations fermées, en plus de la diversification et de l'isolement cytoplasmiques et à la suite de diversifications géniques, une transformation puisse intervenir qui amènerait finalement à des modifications des caractéristiques déterminées par des gènes. Ces hypothèses doivent encore être confirmées par l'expérimentation et l'observation de populations géographiquement dispersées.

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