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Inversion Polymorphism and Phylogeny in *Drosophila*

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Abstract:Drosophila* is an important biological model which has been extensively used in various kinds of studies such as genetics, evolution, cytogenetics, molecular biology, disease biology, ecological genetics etc. It possesses a number of advantages which make it very suitable for such studies. Chromosomal polymorphism due to paracentric inversions which do not include centromere is very common in *Drosophila*. It has been proved to be an adaptive trait and maintained by natural selection. Ecological niche hypothesis states that inversion polymorphism in *Drosophila* is a device to cope with the diversity of environments. Paracentric inversions are of three types: independent, included and overlapping. The overlapping inversions which are found in certain species have interesting properties and are used to discuss their phylogeny. If there are three arrangements in a chromosome involving overlapping inversion, the first can give rise to second or can arise from second through a single inversion. The same is true for second and third, However, the third can arise from the first or vice versa, only through the second arrangement as the probable intermediate step in the line of descent. In case, only third and first arrangements are found in natural population of a species, it is likely that the second remains to be discovered or it existed in the past. In a population, if all the three arrangements occur it is certain that first and third are related through the second arrangement. Based on this theory of overlapping inversions, the gene arrangements which were predicted, were subsequently found in nature. Inversion phylogeny has been discussed in three species of *Drosophila*: *D. azteca*, *D. pseudoobscura* and *D. persimilis.

***Index Terms:Drosophila*, inversion polymorphism, types of inversions, overlapping inversions, inversion phylogeny.**

I. INTRODUCTION

Among different model organisms used to study genetics, such as Saccharomyces cervisiae (yeast), *Drosophila* melanogaster (fruit fly), *Caenorhabditis elegans* (nematode worm), *Xenopus tropicalis* (Western clawed frog), Mus musculus (mouse) and *Danio rerio* (Zebrafish), *D. melanogaster* is probably the best biological model which was used in genetical studies for the first time by T H Morgan in 1909. Since then it is being utilized for research in different areas of biology such as genetics, cytogenetics, developmental biology, population and evolutionary genetics, animal behavior, ecological genetics, evolution, molecular biology, association with Wolbachia endosymbiont, and in the study of certain diseases in humans. It is commonly known as fruit fly or vinegar fly. It is also used in teaching for demonstration of certain basic principles of genetics such as Mendelism, sex-linkage, linkage and crossing-over, gene mapping, detection of mutations etc.

Genus *Drosophila* belongs to the family Drosophilidae (class-Insecta, order-Diptera) and it is characterized by rich species diversity at global level as well as in India. There are more than 1500 species described at global level. About 150 species are reported from India which includes new species and as well as new records (Gupta, 2005; Singh, 2015). There are more than 500 species found at Hawaiian Islands which provides unique opportunity to study evolution in the genus Drosophila (Carson, 1971).

Although *Drosophila melanogaster* is most commonly used species in various kinds of studies, there are other species, such as *D. ananassae, D. bipectinata, D. nasuta, D. malerkotliasna, D. pseudoobscura, D. persimilis, D. subobscura, D. robusta, D. willistonini, D. funebris, D. pavani*, Hawaiian species etc. have also been used by numerous investigators for various kinds of studies at global level. In 2024, an e-resource book for laboratory experiments at under- and post-graduate levels and for research projects in biology courses has been published by Lakhotia and Ranganath (2024) which is very useful for students as well as researchers to follow the protocols of different experiments using *Drosophila malanogaster* and other species.

II. ADVANTAGES OF COSMOPOLITAN SPECIES:DROSOPHILA MELANOGASTER

Drosophila flies possess a number of advantages which make them suitable for experimental studies which are shown below:

(1) Short generation time- in about ten days at about 25 degree temperature, egg develops to adult.

(2) It is very easy to maintain the flies in the laboratory.

(3) The culture medium requires yeast powder, maize powder, agar agar, nepagin, propionic acid which are cheap requirements.

(4) Flies are small which permits easy handling.

(5) A large number of progeny can be produced which is required for statistical accuracy of the experiments.

(6) Flies are harmless and carry no known disease which affects human beings and it does not carry piercing or biting mouth parts.

(7) In every generation, sex ratio remains approximately 1:1.

(8) There is rich species diversity in the genus Drosophila and more than 1500 species are known to occur at global level. In future many more species may be described.

(9) Drosophila flies are found throughout the world. D. melanogater and D. ananassae are cosmopolitan and domestic species which are extensively used in various studies.

(10) It is easy to collect the flies from natural populations and bring them in good condition back to the laboratory.

(11) A large number of mutations are available in D. melanogaster and other species which may be used for gene mapping and linkage studies.

(12) Cytogenetic constitution: It has low number of chromosomes. The regular complement of chromosomes consists of eight chromosomes (diploid number): three pair of autosomes and a pair of sex chromosomes (XX in female and XY in male). There are giant chromosomes or polytene chromosomes in certain tissues of larvae such as salivary glands, gut epithelium, fat bodies and Malpighian tubules which are extensively used in various kinds of cytogenetic studies providing an opportunity to examine directly the nature and functioning of chromosomes in an extended state of interphase. The poletene chromosomes are of large size, homologous chromosomes are permanently synapsed and having specific pattern of bands and interbands. The specific type of banding pattern in these chromosomes facilitates to identify the chromosomes.

Figure 1. Polytene (salivary gland) chromosomes of *Drosophila ananassae* showing six arms radiating from the common chromocentre.

In Figure 1, polytene chromosomes from one nucleus of *Drosophila ananassae* are shown radiating from the common chromocentre which is formed by the fusion of centromeres of all the chromosomes. There are six arms representing XL, XR, 2L, 2R, 3L and 3R (IV chromosomes and Y (male) are very small and remains embedded with the chromocentre. With the help of banding pattern using the polytene chromosome map, each chromosome may be identified. Because of large size, homologous pairing and specific banding pattern, chromosomal aberrations in these chromosomes may be easily identified. In Figure 2, inversions are shown in heterozygous conditions in *D. ananassae.* Since polytene chromosome maps are available in different species of *Drosophila*, chromosomal polymorphism has been extensively studied. Inversions and translocations have been detected in natural populations of different species of *Drosophila*. Inversions are of two types: paracentric (does not include centromere) and pericentric (includes centromere). However, paracentric inversions are more common and has been extensively studied in different species. Dobzhansky (1947) was first to show that inversion polymorphism is adaptive and subject to natural selection. Dobzhansky and his coworkers have suggested the ecological niche hypothesis which states that inversion polymorphism in *Drosophila* is a device to cope with the diversity of environments. The degree and pattern of inversion polymorphism varies in different species of *Drosophila* (Singh, 2019).

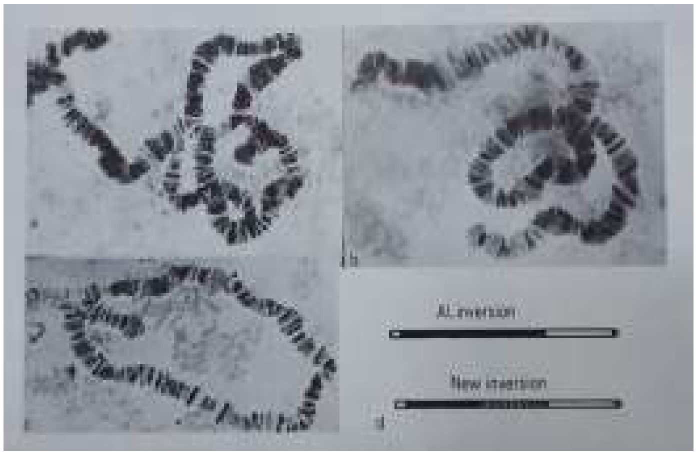

Figure 2.Photomicrographs of 2L of D. ananassae from larvae heterozygous for inversions and diagram of 2L showing location of inversions. (a) pairing between ST and ALin chromosomes, (b) pairing between AL and ALin chromosomes, and (c) pairing between ST and AL chromosomes, (d) diagram of 2L showing

location of inversions. Circle indicates basal end of 2L (Singh, 1983).

III. INVERSION PHYLOGENY

The paracentric inversions in Drosophila are of three types: independent, included and overlapping. Figure 3 shows these three types of inversions. Particulary, overlapping inversions in D. pseudoobscura, D. persimilis and D. azteca arer of special interest because these inversions are used to discuss inversion phylogeny (Dobzhansky, 1951; White, 1973). However, no determination of sequence of origin is possible with independent and included inversions. If we take an example of three arrangements in a chromosome caused due to overlapping arrangements: abcdefghi, aedcbfghi and aehgfbcdi. The first can arise from the second or may give rise to second through a single inversion. For second and third, the same is true. However, the third can arise from the first or vice verca, only through the second arrangement as the probable step in the line of descent. In case, only the first and third arrangements are found in athe past. If all the three arrangements occur in a population, it is certain that the first and third are related through the second arrangement. Thus, the phylogenetic relationships between the three arragements may be shown as:

$1 \rightarrow 2 \rightarrow 3$ or $3 \rightarrow 2 \rightarrow 1$ or $1 \leftarrow 2 \rightarrow 3$ but not $1 \rightleftarrows 3$.

It is interesting to note that with the help of theory of overlapping inversions, the predicted gene arragements were susequently found in natural populations of *D. azreca* and *D. pseudoobscura* (Dobzhansky 1951; White 1973). In *D. azteca*, overlapping inversions are known in the A chromosome. There are seven sequences: alpha, beta, gamma, delta, epsilon, zeta and eta. Figure 4 shows the phylogenetic relationships between different gene arragenents caused due to overlapping inversions in *D. azteca*. These sequences may be arranged in a linear phylogenetic sequence except delta which forms a side branch. It is very important to note that the arrangement zeta was infact predicted using this method of phylogeny and found later (Dobzhansky, 1951; White, 1973). It provided the justification of this method of deriving phylogenertic relationship of overlapping inversions in *Drosophila*. In this case, there is no way to know that which of the seven arrangements is original one.Thus, it shows phylogeny in a limited sense.

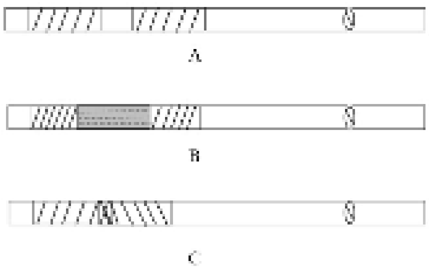

Figure 3. Types of inversions: (A) Independent inversions (B) Included inversions and Overlapping inversions.

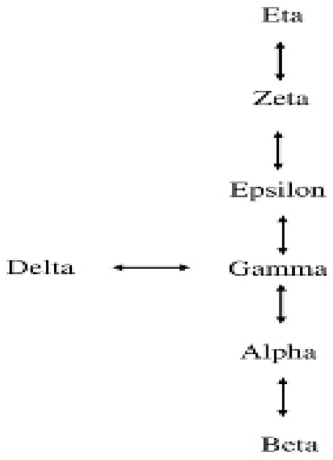

Figure 4. Pnylogenetic chart of overlapping inversions in Drosophila azteca (adapted from White 1973).

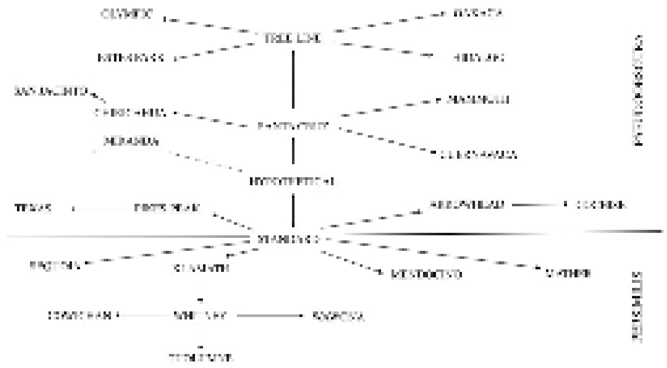

Figure5. Phylogenetic chart of overlapping inversions in the third chromosome of *Drosophila pseudoobscura* and *Drosophila* persimilis (Adapted from Dobzhansky, 1951).

There ia a pair of sibling species: *D. pseudoobscura* and *D. persimilis* occuring in USA. Population genetics of these species with particular referebce to invetrsion polymorphoism has been extensively studied by Dobzhansky and his collaborators (Dobzhansky, 1970). In both these species, a large number of paracentric overlapping inversions are found in the third chromososome and their phylogenetic relationships are shown in

Figure 5. In *D. pseudoobscura* and *D. azteca*, the existenxe of previously unknown sequences was predicted with the help of theory of overlapping inmversions were subsequently found in natural populations. The phylogenetic relationships between overlapping inversions in *D. pseudoobscura* and *D. persimilis* has been discussed in detail by Dobzhansky (1951). One gene arrangement that is Standasrd is common in both these species. All these sequences were derived from each other and related by overlapping inversions. Each sequence is designated by the name of locality in which it was found first. Any two sequences connected by an arrow give a single heterozygous inversion loop. Some gene arrangements which were suggested theoretically based on this theory as missing links between the arrangements were discovered later when more populations were analysed. It is interesting to note that one sequence remains hypothetical considering both the sibling species, however, one sequence having the essential features of this hypothetical one has been found in an other species, *D. miranda* which is related to *D. pseudoobscura* and D. *persimilis.*

CONCLUSION

Thus, chromosomal polymorphism caused due to paracentic invetrsions in *Drosophil*a is an unique feature. It is considered as a decice to cope with the divetrsity of envirnments. There are three types of paracentric inversions: independent, included and overlapping inversions. In certyain species of *Drosophila*, the overlapping inversions have been used to discuss the phylogenetic relationsahips between inversions. It is interesting to note that in *D. pseudoobscura* and *D. azteca*, the existenxe of previously unknown sequences was predicted with the help of theory of overlapping inversions were subsequently found in natural populations.

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