Dobzhansky and Evolutionary Cytogenetics

Pioneering Evolutionary Studies with Chromosomes

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Living organisms continuously attempt to adjust to the environment. If this adjustment occurs in a beneficial way, it is called adaptation. Certain individuals might possess characteristics that better fit the environment and consequently such individuals survive longer and reproduce more. If these beneficial traits are hereditary, such adaptation results in evolution. In course of time, evolutionary forces can also bring about changes in adaptation and in diversity.

Since 1930's and in the following decades, evolutionary biologists such as Dobzhansky, Fisher, Ford, Haldane, Wright, Mayr and many others emphasized the presence of genetic polymorphism in all natural populations and how populations use this reservoir of genetic variability for their evolutionary 'needs'. Theodosius Dobzhansky (1900-1975), an outstanding evolutionist of the 20th century, made seminal contributions to our understanding of evolutionary processes. He explored various facets of evolution empirically, both in the field and in the laboratory; this article mainly focuses on his fascinating works on the adaptive significance of chromosomal polymorphisms.

In the 1920's and 30's, chromosome research gained momentum and the integration of chromosomal and genetic findings gave birth to a new discipline known as 'Cytogenetics'. By then, *Drosophila* was already established as an excellent model system for genetic research (see *Resonance*, Vol. 4, No. 2, 48-52, 1999). Dobzhansky was greatly influenced by the advancement of *Drosophila* genetics and cytogenetics since the early days of his genetics work in Russia until 1936 when he began to work on *Drosophila pseudoobscura*. Let us now find out the role of chromosomal rearrangements in evolution and then we'll see how

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chromosomal rearrangements were elegantly used by Dobzhansky to address evolutionary questions.

Evolution cannot progress in the absence of genetic variability. The primary sources of variability are mutation (alteration of genetic material) and recombination. Variability is further enhanced when chromosomes (which carry genetic material) undergo modifications in their structures. One example of such chromosomal rearrangement is what is called 'inversion'. Chromosomes occasionally break and then get reassembled in various ways. If there are two break points and if the middle piece rotates by 180^0, it results in a chromosomal inversion. In *Drosophila*, such inversions are very easy to analyse in polytene chromosomes, which are giant chromosomes about 150-200 times larger than normal metaphase chromosomes (see *Resonance*, Vol. 2, No. 8, pp 41-49, 1997). This unusual size of the polytene chromosomes is particularly useful to detect any irregularities caused due to structural rearrangements, even under a light microscope. In one species of fruitfly, *Drosophila pseudoobscura*, Dobzhansky discovered the adaptive significance of various chromosomal inversions located on the third chromosome. We will now look into his experimental findings and the impact of his evolutionary interpretations.

Dobzhansky and his colleagues studied different types of chromosomal inversions in wild populations of *Drosophila pseudoobscura* in the southwestern United States and estimated their frequencies from 1932 to the mid-1940s. Each type of chromosomal rearrangement (banding sequence of inversion) is known by its native name, generally abbreviated to two letters. In evolutionary literature, the three most widely discussed types are 'Standard' (ST), 'Arrowhead' (AR) and 'Chiricahua' (CH). These chromosomal variants can easily be detected in the polytene chromosomes either by the formation of inversion loops in the 'heterozygotes' (see *Figure* 1), or by the detailed examination of sectional reversals in the known sequence of band-interbands in the 'homozygotes' (for conceptual details about 'homozygotes', 'heterozygotes' and related terminologies, see

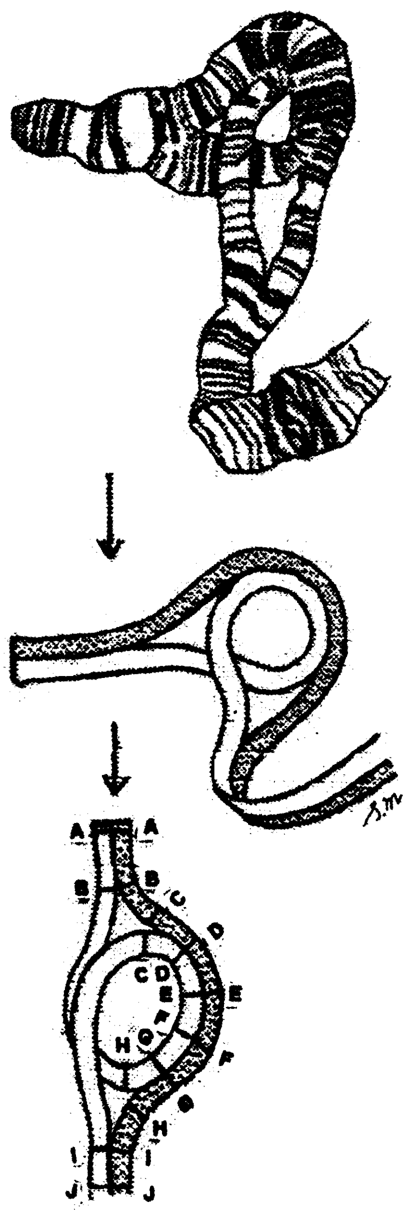

***Figure 1.** A schematically drawn portion of the polytene chromosome showing a typical 'loop' caused during meiotic pairing of homologous chromosomes by an inversion in a heterozygote where out of two homologous chromosomes (paternal and maternal homologues), one has an inverted segment (shown with arbitrarily chosen loci CDEFG). Regions without any inversion (AB or IJ) show perfect pairing (synapsis).*

Resonance, Vol. 4, No. 2, 48-52, 1999; No. 10, 78-87, 1999).

Dobzhansky found different geographic distributions for different types of chromosomal rearrangements (see *Figure* 2), apparently because of their varying Darwinian fitness in different habitats. Thus AR is established throughout California and extends as far as Colorado and New Mexico; ST is found all over California, while CH is prevalent only in Chihuahua and Mexico and its frequency diminishes from Utah, Arizona to westwards along the Pacific coast. Dobzhansky and his colleagues skillfully combined the methods of genetics and ecology and obtained direct evidence to demonstrate the adaptive significance of the inversion polymorphisms in *Drosophila*. They found that the frequencies of particular chromosomal rearrangements were correlated with the cyclic changes of season and with altitude. Thus, the frequency of inversions varies in space as well as in time. Let us now ask the question: what is the genetic basis of such adaptation?

Chromosomal inversions are known to suppress crossing over (exchange of genetic material during meiotic cell division that occurs during gamete formation) between the genes located within the inverted region. This is because of the mechanical constraints caused by the loop formation when chromosomes start pairing during cell division. Interestingly, if an 'inverted region' of chromosome includes a combination of

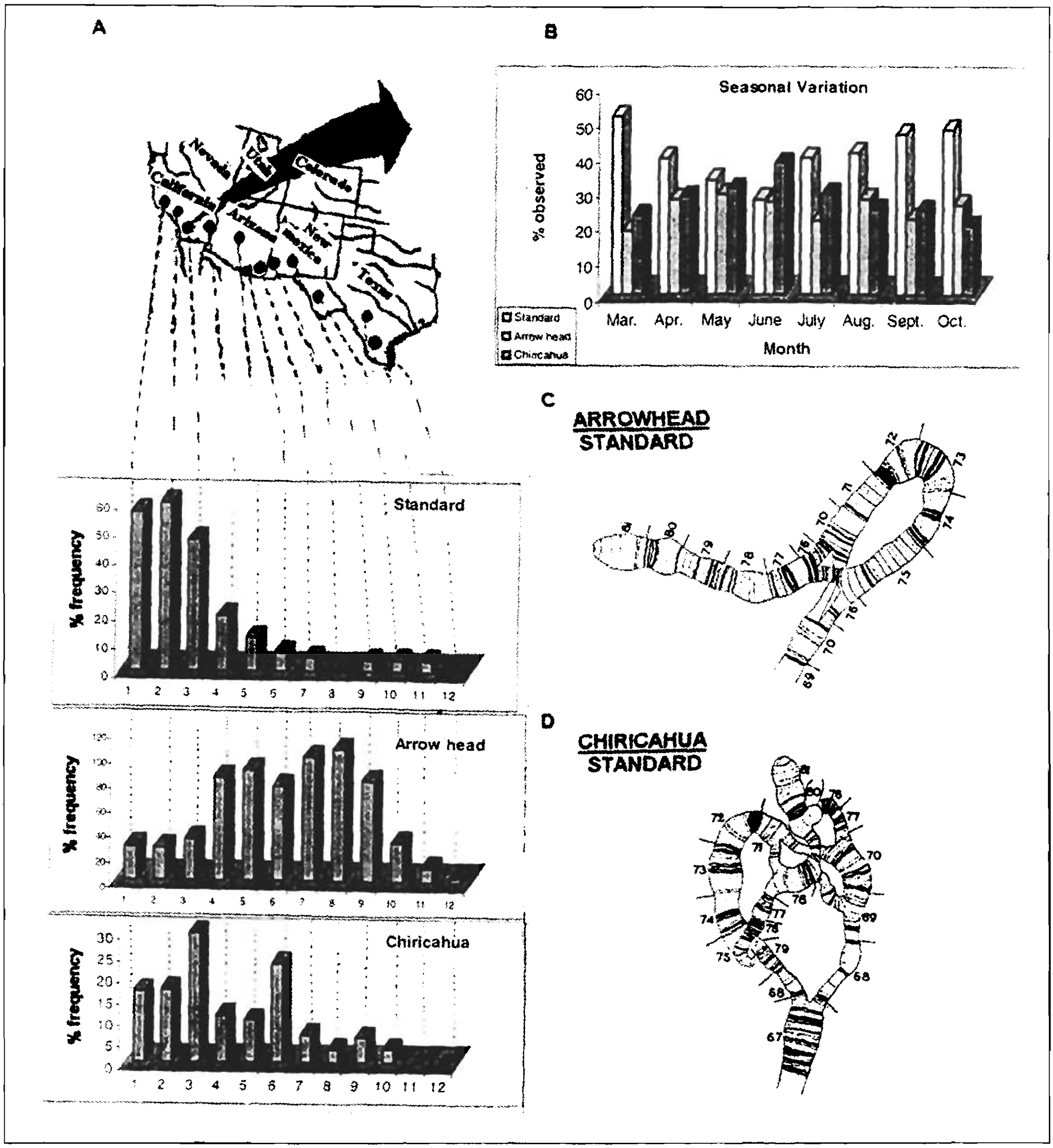

Figure 2. A) Frequencies (%) of three different third chromosome gene arrangements in Drosophila pseudoobscura in twelve ecological habitats along the United States–Mexican border. (Adapted and graphs reconstructed from Dobzhansky 1944). B) Frequency (%) of different third chromosome arrangements in D. pseudoobscura found at different months in one of the localities (see arrow), Mount San Jacinto, California. (Adapted and graphs reconstructed from Dobzhansky 1947). C, D) Two common third chromosome arrangements found in the inversion heterozygotes of D. pseudoobscura (AR/ST & CH/ST, see text for details). (Adapted from Dobzhansky and Sturtevant 1938).

genes which is beneficial (adaptive) in a particular environment, the inversion will tend to be maintained in that population. The adaptive success of an inversion is thus often based on its ability to maintain the advantageous gene combination by preventing the 'beneficial' genes reassorting themselves into less advantageous combinations during 'crossing over'.

The advantage of certain combinations of genes 'trapped' within an inverted loop was further demonstrated by Dobzhansky in laboratory experiments. He reared flies with various chromosomal inversions in population cages and simulated different conditions of temperature, humidity and food-supply. He estimated relative fitness for individuals having different chromosomal rearrangements and calculated 'selective pressures'. Dobzhansky demonstrated adaptive values associated with each type of inversion under different environmental conditions. In later years, Dobzhansky's pioneering technique became an excellent method for the experimental study of natural selection in many populations.

Dobzhansky's cytogenetic approach proved to be of great value since for the first time it explained evolutionary significance of chromosomal rearrangements in natural populations. Dobzhansky further established that polymorphic variations are adaptive in nature and that populations can adjust to specific environments at specific times. Using 'chromosomal rearrangements' as a tool for evolutionary analysis, Dobzhansky and his colleague Pavlovsky found experimental evidence for many other evolutionary processes such as 'genetic drift' via 'founder principle'. Dobzhansky's work has inspired the next generation of scientists, and evolutionary cytogenetics, along with molecular methodologies, continues to be an exciting area of evolutionary research. In fact, Dobzhansky's stunning pronouncement that "nothing in biology makes sense except in the light of evolution" has 'unified' biologists, at least conceptually. A leading contemporary evolutionist, Stephen Jay Gould did not exaggerate when he extolled Dobzhansky as "the greatest evolutionist of our century."

Suggested Reading

[1] M B Adams (ed.), *The Evolution of Theodosius Dobzhansky*, Princeton University Press, 1994.

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[5] T Dobzhansky, Genetics of Natural populations XIV, A response of certain gene arrangements in the third chromosome of *Drosophila pseudoobscura* to natural selection, *Genetics*, 32, 142-160, 1947.

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