

In Memory of Danko Brncic, a friend

En memoria de Danko Brncic, un amigo

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I do not intend to write a scholarly article in memory of my friend, Danko Brncic. Suffice it to say that during my daughter's trip to Chile where she studied the blood physiology of Humboldt penguins, Danko provided the safety net in case anything went wrong in the field: broken bones or debilitating illnesses, for example. I was sorry to learn recently of Danko's death.

Brncic was one of Dobzhansky's early students who undertook to study "co-adaptation". Dobzhansky and Wright had earlier reported on the equilibrium frequencies of chromosomal inversions that were established in laboratory populations of *Drosophila pseudoobscura* maintained at 25 °C. These equilibria were established when chromosomes of the contrasting gene arrangements came from the same geographic locality. Later experiments involving chromosomes of different gene arrangements each of which came from a different geographic locality gave different results. In these inter-locality populations, one gene arrangement tended to displace the other. Assuming (for good reason) that equilibria revealed the selective superiority of inversion heterozygotes, Dobzhansky concluded that within a locality, inversions are co-adapted in the sense that their heterozygotes have superior fitness. In contrast, flies heterozygous for inversions that come from

different localities do not exhibit a corresponding heterosis. In effect, Dobzhansky suggested that heterosis was the outcome of natural selection, of a co-adaptation of the gene content of different gene arrangements. As Dobzhansky's post-doctoral student during the early 1950s, Brncic undertook to demonstrate co-adaptation within the arrowhead gene arrangement; he succeeded. I have provided a detailed analysis of Brncic's results in both topics in population genetics (1968) and basic population genetics (1981).

A quarter-century ago the matter of coadaptation stirred considerable discussion. One of the supporting pieces of evidence was provided by Dobzhansky's student, Wyatt Anderson, who studied body size *Drosophila pseudoobscura* Ries carrying recombinant and non-recombinant chromosomes (1968, *Genetical Research* 12:317-330). This study followed a corresponding one carried out in Great Britain by A. M. MacFarquhar and F. M. Robertson using body size in *Drosophila subobscura*, as a measure of heterosis (1963, *Genetical Research* 4:104-131). The earlier experiment failed to reveal any heterosis or its loss of following gene recombination. The contrasting results of these two studies are mentioned in the following untitled essay—nearly four decades after their original publication.

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