

there is every reason to suggest that the trait is controlled by an extranuclear factor.

Most facts here reported might be explained if such a factor were scarce and its replication rate were slower than the cellular division rate, so that it could be lost in certain cellular lines but not in others within an individual. Further tests to probe the hypothesis are already in progress.

David, J.R., M. de Scheemaeker-Louis and E. Pla. Laboratoire de Biologie et Génétique Evolutive du CNRS, Gif-sur-Yvette, France. Evolution in the seven species of the *Drosophila melanogaster* subgroup: comparison of the electrophoretic mobility of the enzymes produced by the Adh locus.

Alcohol dehydrogenase (Adh) of *Drosophila melanogaster* is an extensively studied enzyme for several reasons. It has been possible to relate the enzymatic function with a physiological trait, ethanol tolerance. This phenotypic property has a strong adaptive significance in the ecology of wild populations. Finally the worldwide polymorphism known at the Adh locus seems to be maintained by natural selection. The F

allele, producing a fast migrating protein, has a higher activity than the S allele and is most frequent in temperate countries where the alcohol tolerance is higher (see David, 1976 for a review). Apart from the two widespread Adh<sup>F</sup> and Adh<sup>S</sup> alleles, three other rare ones have also been found in natural populations.

At the present time six other species are known in the *D. melanogaster* taxonomic subgroup; these include the cosmopolite *D. simulans* and five others, endemic in the Ethiopian region. Up to now only the Adh of *D. simulans* has been studied and the species is known to be generally monomorphic for a very slow allele, having some analogy with the US allele found in an African population of *D. melanogaster*. It seemed therefore interesting to compare the mobility of Adh found in the different species with that of the five alleles available in *D. melanogaster*.

Results are presented in Fig. 1. In order to improve electrophoretic discrimination, the various alleles were ordered according to their decreasing anodal mobility. In all cases, the electrophoretic pattern was the same: for a homozygous strain, we observe two isozymes which correspond to conformational differences of the dimer molecule; the activity of the slower isozyme is always higher. Moreover, treatment of flies with acetone (not shown) resulted in all cases in the disappearance of the slow migrating isozyme and in the increase of a third, still faster migrating, band. There is therefore almost a complete certitude that the enzymes shown in Fig. 1 are the product of the same, homologous locus, in all species.

It is well known that a single electrophoretic technique reveals only part of the effective genetic variability. In the present case, it is striking that ordinary starch gel electrophoresis was sufficient for showing a significant difference between all alleles. In some cases, the difference of migration is very small (1 mm) but it proved to be always the same in different runs.

Five alleles were found in *D. melanogaster*, the most extensively studied species. By contrast, all the other species were observed to be monomorphic. This last conclusion, however, cannot be considered as being strongly established because only a small number of laboratory strains were studied. Present data seem, however, to allow several conclusions.

First the Adh locus, at least in that group of species, can be considered as a fast evolving gene. As previously stated, the enzyme produced is involved in ethanol detoxification and big differences are observed in ethanol tolerance of the various species (David et al. 1974). Perhaps this diversification of the ecological niche with respect to environmental alcohol is related to the occurrence of different alleles in the different species.

Second, a proportion of 100% of unique alleles is observed here so that the enzyme seems to have an absolute diagnostic value for a specific identification. In a recent paper (Throckmorton, 1978) indicated that, when studying phylogenetic relationship between related species, an average of 30% of unique alleles was observed. The much higher proportion found here is probably a singularity of the locus here studied.

Third, a general problem in speciation studies is to establish whether the electrophoretic alleles occurred before or after the specific divergence. In the present case we can state that the apparition of the new alleles and their fixation almost certainly occurred after the specific separation.



Fig. 1. Electrophoregram of Adh stained with isopropanol after starch gel electrophoresis (discontinuous buffer system of Poulik, 1957). From left to right: *D. yakuba*; *D. melanogaster* allele Ultra Slow; *D. simulans*; *D. melanogaster* Slow; *D. teissieri*; *D. mauritiana*; *D. orena*; *D. melanogaster* Fast; *D. melanogaster* F<sub>1</sub>; *D. erecta*; *D. melanogaster* Ultra Fast.

Phylogenetic relationships between the various species were recently worked out using polytene chromosome structures (Lemeunier and Ashburner, 1975). Results here presented suggest that the genetic distance between the various species could be high. Of course, analysis of a single gene provides little information and studies of other loci are in progress.

References: David, J. 1977, *Année Biol.* 16:451-472; David, J., F. Fouillet and M.F. Arens 1974, *Arch. Zool. exp. gén.* 115:401-410; David, J., F. Lemeunier, L. Tsacas and C. Bocquet 1974, *Ann. Génét.* 17:235-241; Lemeunier, F. and M.A. Ashburner 1976, *Proc. R. Soc. Lond. B* 193:225-294; Poulik, M.D. 1957, *Nature* 180:1477; Throckmorton, L.M. 1978, *Beltsville Symposium in Agricultural Research*, Wiley and Sons, N.Y. 221-239.

Davis, B.K. Virginia Polytechnic Institute and State University, Blacksburg, Virginia. Mutants which cause abnormal rotation of the abdomen or genitalia.

A surprising number of loci can mutate to affect the development of the abdomen or genitalia in *D. melanogaster* such that the adult structures are out of alignment with the rest of the body. A study of the twisted locus

(Davis 1975; Davis, DIS this issue) led to a search through the "Genetic Variations of *D. melanogaster*" (Lindsley and Grell 1968), aided by "The Mutants of *D. melanogaster* Classified According to Body Parts Affected" (Braver 1956). Although this search was not exhaustive for the main source (Lindsley and Grell 1968) and did not include current literature, it revealed 15 loci with one or more alleles reported to cause rotation of the genitalia or the abdomen (Table 1).