Besides lacking 2 of the bands present in Imperial rye (No. 4 and 7), the amphiploid possessed a band (No. 5) not present in either parent cultivar. These differences in pattern could be due either to an interaction between wheat and rye proteins when in a common cytoplasm or simply to the Imperial rye used as a control in the present study differing in genotype from the rye plant used in constructing the amphiploid. The latter explanation is favoured[8] because it was found that the pattern of rye bands in F_1 seeds derived from crossing Chinese Spring with the Imperial rye control resembled the pattern of the rye parent rather than that of Sears' amphiploid. However, irrespective of the cause of the pattern difference, it is clear that the gene(s) controlling all of the rye bands expressed in the amphiploid are located on rye chromosome E, since the pattern of the chromosome E addition line was identical with that of the amphiploid (Figure 2).

To summarize, it is evident that the gene(s) controlling all of the slow-moving proteins of diploid King II rye, and probably Imperial rye also, are located on one particular rye chromosome, whereas in hexaploid Chinese Spring wheat the genetic control of these proteins is associated with at least 2 chromosomes of each genome. It is concluded that the genome of rye must have evolved along a separate pathway from that of the 3 wheat genomes, since it is widely accepted that a change in the number of loci controlling a protein phenotype is a reliable index of evolutionary divergence[9,10]. On the other hand, evidence from studies of chromosome homoeology indicates that the rye and wheat genomes have most likely been derived from a common ancestral genome[3]. To account for these separate findings it is postulated that the gene(s) controlling the slow-moving proteins in the original diploid ancestor of the Triticinae were located on only 1 of the 7 chromosomes, and that rye was derived from this species. Further it is suggested that a descendant of this ancestral diploid acquired two-chromosome control of these proteins, possibly by a process of gene duplication and chromosome translocation, analogous to that suggested for the origin of the α, β, γ and δ polypeptide chains of haemoglobin[9], and that the wheat genomes have come from this derived species.

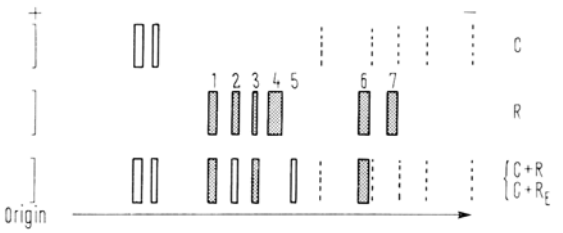

Fig. 2. Diagram of starch-gel electrophoretic patterns of slow-moving proteins extracted in 0.01 M sodium pyrophosphate from Chinese Spring wheat (C), Imperial rye (R), the amphiploid (C + R) and rye chromosome E addition line (C + R_E). Electrophoresis for 7.5 h at 11.5 V/cm. (Shaded rectangles, strong bands; clear rectangles, weak bands; dotted lines, faint bands often difficult to detect.)

If this model is correct, the chromosome segments controlling the slow-moving proteins in wheat and rye would be related by descent and, consequently, the respective proteins would be expected to have similar amino acid sequences and similar chemical properties. However, the different behaviour of these proteins during pyrophosphate extraction seemed to be inconsistent with this expectation, and a quantitative study of their solubility in pyrophosphate buffer was made to resolve this anomaly. It was found that although the slow-moving proteins of rye are more soluble in this buffer than those of wheat, the difference is small and probably does not represent a fundamental difference in their chemical properties[11].

The proposed pathway for the evolution of wheat and rye genomes obviously needs further testing and additional data are expected to come from determining the number of chromosomes controlling endosperm proteins in other genomes within the Triticinae or, ideally, comparing the amino acid sequences of the proteins involved[12].

Résumé. En comparant les diagrammes d'électrophorèse en gels d'amidon de gliadine obtenus à partir d'un blé hexaploïde, d'un seigle diploïde et de blé + seigle amphiploïdes avec les lignes d'additionnement des chromosomes blé-seigle on constata qu'un chromosome de seigle contrôle toutes les gliadines du seigle.

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[8] A similar explanation may account for the faint band (No. 4, Figure 1) which was observed consistently in the pyrophosphate extracts from Holdfast + King II amphiploid and the chromosome V addition lines, but which was absent from the wheat and rye controls.

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[12] The authors would like to thank Miss B. M. Simons for technical assistance. Financial support from the Wheat Industry Research Council is gratefully acknowledged.

Modes of Variation in Alcohol Dehydrogenase in *Drosophila melanogaster*

It has previously been shown[1-3] that crude enzyme extracts of the two naturally occurring electrophoretic variants of *Drosophila melanogaster* alcohol dehydrogenase can differ in their thermolabile properties and specific activities. We have compared Adh alleles extracted from sternopleural selection lines maintained by Prof. A. Robertson, from a cage population polymorphic for Adh alleles initiated by Prof. J. A. Beardmore, and also Adh alleles originally isolated by Prof. E. H. Grell and subsequently put on a common genetic background.

Homogenates of 20 third instar larvae in 1 ml 0.05 M orthophosphate buffer were centrifuged at 30,000 g for 20 min. The supernatants were assayed for alcohol dehydrogenase activity in a Perkin-Elmer 124 spectrophotometer at 25 °C by timing the change in 0.1. O.D. units at 340 nm associated with the reduction of nicotinamide adenine dinucleotide (NAD) using isopropanol as

substrate. Following the normal assays the extracts were incubated at 40 °C in a water bath for 10 min and then reassayed. Total protein in each extract assayed was determined by a modification of the Folin technique[4].

The results (Table) show that Adh alleles extracted from different populations have different specific activities although within a population the extracts of AdhF homozygotes have higher enzyme activities than extracts of AdhS homozygotes. The enzyme activity of extracts of heterozygotes relative to the parental homozygotes varies and in three instances is significantly different to the mid-parental value.

Enzyme extracts of AdhF homozygotes in each population are more thermolabile than extracts of AdhS homozygotes. However there is considerable variation in thermolability between enzyme extracts of AdhS homozygotes from different populations, the AdhS enzyme from BEARDMORE's population being considerably less heat stable than AdhS enzyme extracts from either ROBERTSON's or GRELL's stocks.

After heat treatment enzyme activity in extracts from G.AdhF/G.AdhS heterozygotes is significantly higher than the enzyme activity in heat treated extracts of either of the 2 homozygous parents[2]. Although the R.AdhF/R.AdhS enzyme extract is as heat stable as the extract of R.AdhS homozygotes the enzyme activities remaining after heat treatment are not significantly different.

Of the 4 heterozygotes between alleles extracted from BEARDMORE's population only one has significantly higher enzyme activity after heat treatment than either of the heat treated parental extracts. It is interesting that although both AdhS alleles from this population have similar specific activities and thermolabile properties in homozygotes they have different thermolabile properties in heterozygotes with B.AdhF, one losing 70% of activity and the other 86%.

No attempt was made to control the genetic background of the alleles extracted from either BEARDMORE's or ROBERTSON's populations. However BEARDMORE's cage population had been established for 3 years prior to the extraction and it seems likely that the genetic background of the Adh alleles from this population would be uniform. Each of the 4 AdhF alleles tested from these 3 populations were phenotypically identical after electrophoresis on polyacrylamide gels run at different pH as also were the 4 AdhS alleles tested. Similarly there was no variation in electrophoretic mobility between the 6 heterozygotes tested.

These data show that there are at least 3 modes of variation in alcohol dehydrogenase in *D. melanogaster* populations. There are 2 naturally occurring electrophoretic variants which circumstantial evidence indicates are determined by different alleles at the same locus. In addition there is variation in enzyme activity and thermolabile properties both within and between electrophoretic forms which may be due either to structural gene differences or to background modification.

HARRIS[5] has discussed some of the ways in which the polypeptide determined by a particular gene can subsequently be modified to give rise to enzyme molecules which are electrophoretically distinguishable. Similarly, modification of the polypeptide after translation might affect other properties of the enzyme without altering the electrophoretic mobility and may, at least in part, be the explanation for some of the variation described in alcohol dehydrogenase activity.

These data further indicate that the proportion of polymorphic loci estimated in populations of many different organisms by electrophoretic techniques to be about 30%[5,6] may considerably underestimate the total variation present. One aspect of the phenotype on which natural selection will not operate is electrophoretic mobility per se and in terms of selection, variation in electrophoretic mobility may be less important than variation in other properties of the enzyme which are not necessarily correlated with the charge on the enzyme molecule. Thus, although the same electrophoretic form of an enzyme may exist in two or more populations, it is conceivable that the biochemical properties of this variant may differ between the populations and natural selection may be maintaining the same electrophoretic form for different reasons in different populations[7].

Genotypes	n	Mean specific activities in crude extracts				Activity remaining (%)
		Before heat		After heat		
		$\bar{x}$	S.D. $\bar{x}$	$\bar{x}$	S.D. $\bar{x}$	
BEARDMORE's stocks						
B_1 AdhF	8	3.5	0.123	0.3	0.018	8.6
B_2 AdhF	8	5.7	0.15	0.6	0.039	11.3
B_1 AdhS	8	1.9	0.075	0.3	0.029	15.7
B_2 AdhS	8	1.9	0.068	0.3	0.029	16.4
B_1 AdhF/B_1 AdhS	8	2.9[a]	0.07	0.9[b]	0.18	30.1
B_1 AdhF/B_2 AdhS	8	2.7	0.14	0.4	0.023	14.1
B_2 AdhF/B_1 AdhS	8	3.8	0.23	0.7	0.11	19.5
B_2 AdhF/B_2 AdhS	8	4.3[a]	0.21	0.6	0.074	13.9
ROBERTSON's stocks						
R AdhF	10	8.0	0.37	0.5	0.072	6.7
R AdhS	10	3.4	0.175	1.4	0.092	39.8
R AdhF/R AdhS	10	4.3[a]	0.101	1.6	0.068	38.1
GRELL's stocks						
G AdhF	8	8.5	0.33	1.2	0.092	14.1
G AdhS	8	2.9	0.13	1.5	0.188	54.4
G AdhF/G AdhS	8	5.4	0.32	2.0[b]	0.108	38.4

[a] Heterozygote enzyme activity significantly different to the mid parental value. $p < 0.01$. [b] Heterozygote enzyme activity significantly higher than the enzyme activity in either of the 2 parental homozygotes. $p < 0.01$.

Zusammenfassung. Neben zwei elektrophoretisch verschiedenen Varianten der *Drosophila*-Alkoholdehydrogenase kommen innerhalb dieser Varianten weitere Variationen vor, die sich in ihrer spezifischen Aktivität und Temperaturempfindlichkeit unterscheiden. Es wird daraus geschlossen, dass der Grad des Polymorphismus von Populationen grösser sei, als aufgrund elektrophoretischer Untersuchungen geschätzt wird.

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