

tion of histological data and to a lack of experimental control by some of the older authors. But they can also be ascribed to the existence of a certain degree of sex variability in certain strains: some strains may produce a percentage of true hermaphrodites, as shown in this paper, and some are totally gonochoristic^{12,13}. A possible hybridization between *X. helleri* and *X. maculatus* in aquarium tanks has been accounted as responsible for a labile sex differentiation¹⁵. It has been ascertained however in the present experiments that the gonads of the

protogynous hermaphrodites are oval and not different from the gonads of the pure female individuals, and that the protogynous hermaphrodites do occur in domesticated strains that any aquarium breeder would identify as true swordtails *X. helleri*. Further research should ascertain whether proterogyny is present in natural populations of *X. helleri*.

Xiphophorus helleri: progenies of different virgin females paired with 3 exceptional protogynous hermaphrodites in male phase (♀ 1, 2, 3)

Parents	Number of broods	Offspring		♂♂ (%)
		♂♂	♀♀	
♀ ₁ × ♀ ₁	4	33	78	29.7
♀ ₁ × ♀ ₂	4	18	71	20.2
♀ ₂ × ♀ ₃	4	17	61	21.8
♀ ₂ × ♀ ₄	4	16	70	18.6
♀ ₃ × ♀ ₅	4	22	92	19.3
♀ ₃ × ♀ ₆	4	15	75	16.7

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Developmental G6PD polymorphism in *Drosophila melanogaster*: Evidence for non-structural variants

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Summary. G6PD isozyme variation in *Drosophila melanogaster* is investigated in the larval stage through electrophoretic and genetic analyses. As current structural models for this gene-enzyme system fail to apply in these laboratory populations, the authors suggest a regulatory hypothesis to explain their observations.

The electrophoretic phenotype of G6PD in *Drosophila melanogaster* was shown to have a complex relationship to its structural genes, because of regulatory factors affecting isozyme patterns¹. An association between G6PD isozyme patterns and vestigial marker was also observed and could not be explained in terms of structural genes only²; these studies were performed on adult single fly homogenates. As far as we know, the only available information about G6PD developmental expression is from Steele et al.³, who measured total enzyme activity of larval stage, and Wright and Shaw⁴, who monitored electrophoretically *D. melanogaster* embryos up to the 48th h from deposition. In this communication we report some observations concerning G6PD isozyme pattern in *D. melanogaster* larvae. Our results provide evidence that G6PD electrophoretic variation is inherited in a peculiar non-Mendelian fashion that deserves attention. We sampled 3rd instar larvae from Canton strain, from an unrelated strain carrying the vg marker and from 6 populations having a Canton × vg cross as their common origin, plateaued for a quantitative trait after about 70 generations of selection⁵. We raised these populations in mass culture at 25 °C for several generations, and then took random samples of about 100 individuals in the proper developmental phase. Cellogel electrophoresis was carried out on pooled homogenates of the above 100 flies samples, following the procedure detailed in Pieragostini et al.². As represented in figure 1, samples from vg strain exhibited a fast band, selection lines a slow one; Canton samples gave single bands even slower than selection lines. Canton and vg strain, being genetically unrelated, could reasonably be homozygous for the slow and fast allele

respectively and exhibit single bands; larval stage variation would then be similar to adult stage variation⁶. However, if this were our case, we would expect multiband patterns in the progeny from Canton and vg strain (selection lines); our multiple sampling procedure would certainly reveal the presence of segregational homozygotes with the fast form of the enzyme. Heterozygotes too would give their contri-

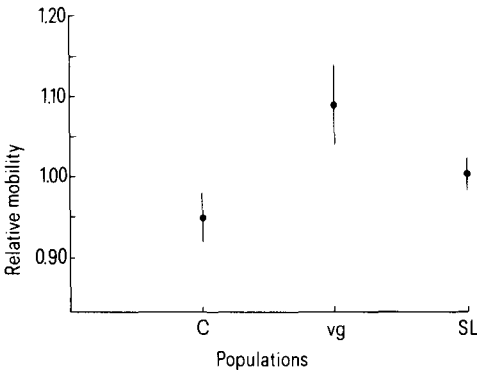


Fig. 1. G6PD phenotypes in larval populations of *Drosophila melanogaster*. From left to right, Canton strain (C, number of samples = 16), vg strain (vg, number of samples = 11), selection lines (SL, including PMvg⁺, PFvg⁺, PKvg⁺, PMvg, PFvg, PKvg, number of samples = 10 each) average mobilities. They are expressed in standard units (mm from origin of samples/mm from origin of standard) and are represented with their 't₉₅' confidence intervals. 2-banded zymograms, in mixed control runs, confirmed non-homology of bands.

G6PD phenotypes in larval progenies from crosses of *Drosophila melanogaster* populations: number of determinations per cross. Assignment to mobility classes was confirmed through control runs of mixed samples

Electromorph mobility	Crosses		PMvg × vg		vg × PFvg		PFvg × vg		vg × PKvg		PKvg × vg	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
1.10	4	...	11	...	6	...	8	...	6	...	9	...
1.00	...	4	...	3	...	3	...	5	...	3	...	5

bution to a multiband pattern, because codominance seems to be the rule in isozyme variation. A Mendelian hypothesis also fails to apply in our further observations of electrophoretic phenotype. In the progeny from vg strain × PMvg, PFvg, PKvg population crosses, neither F₁s nor F₂s exhibit multiband patterns.

Within each generation we did not observe mobility differences among populations, but it is worth pointing out that F₁s show single fast bands of the same mobility as parental vg strain and F₂s single slow bands, the same as parental PMvg, PFvg, PKvg (table). We could interpret this phenomenon as a maternal effect if we could find any difference between F₁ direct and reciprocal crosses: figure 2

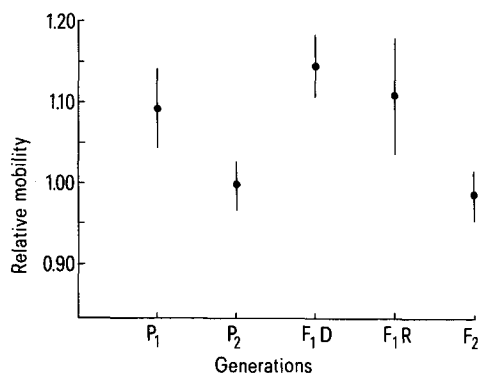


Fig. 2. Comparison between parents and progeny of the cross between electrophoretic variants of larval stage. From left to right, vg population (P₁), averaged PMvg, PFvg, PKvg (P₂), averaged mobilities of 1st generation progeny in direct and reciprocal crosses (F₁D and F₁R), averaged mobilities of 2nd generation progeny (F₂), obtained by random matings within each F₁.

shows that this hypothesis is not verified in our populations. On the basis of these results, we might suggest the existence of regulatory factors affecting the electrophoretic expression of G6PD. They could be contributed by PMvg, PFvg, PKvg populations and favour the appearance of the slow electromorphs; if this regulatory mechanism were unable to operate early on in development, it would not affect F₁ larvae but would do so in F₂ ones; alternatively, vg strain could carry a factor masking the presence of the slow electromorphs in F₁ larvae that is silenced later on.

In any case, the G6PD gene-enzyme system seems to be rich in non-structural variation^{2,5,7}; we intend to continue the analysis of the biochemical and genetic relationships of electrophoretic variants observed in larval populations and in their corresponding pupae and imagoes.

Similar phenomena are reported for other gene-enzyme systems in the recent literature⁸: this kind of information can prove most useful to estimate the relative importance of structural and regulatory variations and evaluate their evolutionary rôle⁹.

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A genetic study of intergradation between *Mytilus edulis* and *Mytilus galloprovincialis*¹

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Summary. A study of geographic variation at 2 diagnostic allozyme loci in the mussels *Mytilus edulis* and *M. galloprovincialis* reveals considerable spatial variation, both in allele frequencies and in the extent of intergradation.

Electrophoretic techniques have been used extensively for the characterisation of variation at protein loci in natural populations^{2,3}, yet considerable problems have arisen in attempts to identify the forces that maintain and modify this variation⁴. Electrophoretic investigation has certain advantages in systematic studies⁵ and has proved powerful and informative in analyses of the genetic structure of hybrid zones⁶⁻⁹. Here we report the results of an electrophoretic survey of populations of the mussels *Mytilus edulis* and *M. galloprovincialis* in the British Isles which provides evidence for a zone of intergradation of unusual complexity.

M. galloprovincialis is confined largely to the Mediterranean, Adriatic, and Black Seas, where it may have evolved¹⁰, but morphological and electrophoretic evidence suggests that it occurs sympatrically and interbreeds with *M. edulis* in S.W. England and Ireland¹¹⁻¹⁵. Its systematic status is uncertain; it has been regarded as a subspecies of *edulis*¹⁶, though in S.W. England good morphological separation and different spawning times provides initial evidence for 2 biological species¹¹.

Samples of adult mussels were collected from the sites given in figure 1 and assayed electrophoretically at 2 diagnostic loci *Est-D* and *Lap-I*. Technical details and