SHORT PAPERS

INHERITANCE DURING PARTHENOGENESIS IN *DAPHNIA MAGNA*

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ABSTRACT

Natural populations of *Daphnia magna* have been found which are polymorphic for electrophoretic variants of supernatant malic dehydrogenase, esterase, and alkaline phosphatase. Using these enzyme variants as genetic markers it has been possible to demonstrate the absence of recombination during parthenogenetic reproduction. Genetic uniformity is expected within parthenogenetic clones derived from a single female.

AMONG most of the species of the genus Daphnia both parthenogenetic and sexual reproduction occur. In natural populations parthenogenesis is the common mode of reproduction and parthenogenetic offspring are normally female. However, in response to certain environmental conditions, in particular crowding (BANTA and BROWN 1929), male offspring are also produced parthenogenetically. At this time or a little later, the females present in the population start producing sexual eggs which must be fertilized if they are to develop.

Genetic uniformity among the parthenogenetic progeny of a single female had been expected as early cytological work (MORTIMER 1936) indicated that only a single, essentially mitotic division occurred during parthenogenetic oogenesis. However, more recent research has indicated that a variable amount of meiotic behaviour precedes this division. OJIMA (1958) observed only a transitory "synaptic concentration" of chromosomes, but in another strain of *D. pulex*, BACCI, COGNETTI and VACCARI (1961) noted pairing of chromosomes and eventually disjunction of the bivalents formed. As polar body formation was suppressed in both instances, recombination will be the only effective means of generating variability among the parthenogenetic progeny.

BACCI *et al.* (1961) assume that crossing over will accompany the chromosome pairing they observe and further suggest that male individuals produced during parthenogenesis are the result of genetic segregation due to this recombination. In this latter supposition they appear to have overlooked several relevant observations. It has long been known that parthenogenetic broods are usually single sexed (CUVIER 1833) and further that the sex of a given brood depends largely upon the environmental conditions to which the mother was exposed (BANTA and BROWN 1929). These observations would seem to indicate that if sex determina-

tion results from recombination then recombination itself must occur only in certain environmental conditions, and even then the difficulty of explaining single-sexed broods remains. Nevertheless if BACCI *et al.* (1961) are correct then segregation for genetic markers should be observed during parthenogenesis. The present study tests this possibility.

Earlier genetic studies on the genus Daphnia have been hindered by the inability to obtain suitable markers. Thus, interpretation of BANTA's work (1939) on *Daphnia longispina* is difficult as the mutants he utilized were of low penetrance and showed pronounced maternal effects. Ideally, for a study of recombination during parthenogenesis, completely penetrant, codominant alleles at a given locus should be used. Visible mutations of this kind are rare, but protein polymorphisms demonstrated by electrophoresis often satisfy these requirements.

MATERIALS AND METHODS

Using 7% polyacrylamide gels and a modified Ornstein-Davis (1964) buffer system, populations of *Daphnia magna* have been screened for electrophoretic variants of several enzyme systems. Single females from each population were crushed in a drop of water and the homogenate absorbed on filter paper discs. The gels were run for 80 min at a constant current of 3 m.a. per tube and were then stained using methods similar to those of HUBBY and LEWONTIN (1966).

RESULTS AND DISCUSSION

Electrophoretic variants were detected for supernatant malic dehydrogenase, esterase and alkaline phosphatase (Figure 1). In order to prove that the electrophoretic variants were genetically determined, sexual crosses were made between known phenotypes and the offspring scored for their electrophoretic phenotypes (Table 1). In each case, the observed phenotypic ratios among the sexual progeny were in close agreement with the expected proportions assuming that the electrophoretic variants were the products of codominant alleles at a single locus.

If recombination occurs during the development of parthenogenetic eggs, then a number of homozygous individuals should be included among the progeny of females heterozygous for an enzyme variant assuming the enzyme locus is not tightly linked to the centromere. To test this possibility, females from a population polymorphic for malic dehydrogenase (MDH) variants were separately

TABLE 1

Sexual reproduction

Enzyme	Parental phenotypes	Progeny phenotypes	Fit to expected frequencies
Malic dehydrogenase	M/F ♀ ♀ × M/F ♂ ♂	27 FF 51 M/F 24 MM	$\chi^2_2 = 0.176$ $P > .9$
Alkaline phosphatase	S/F ♀ ♀ × S/F ♂ ♂	20 FF 47 S/F 24 SS	$\chi^2_2 = 0.456$ $P > .7$
Esterase	S/F ♀ ♀ × F/F ♂ ♂	42 FF 46 S/F 0 SS	$\chi^2_1 = 0.182$ $P > .5$

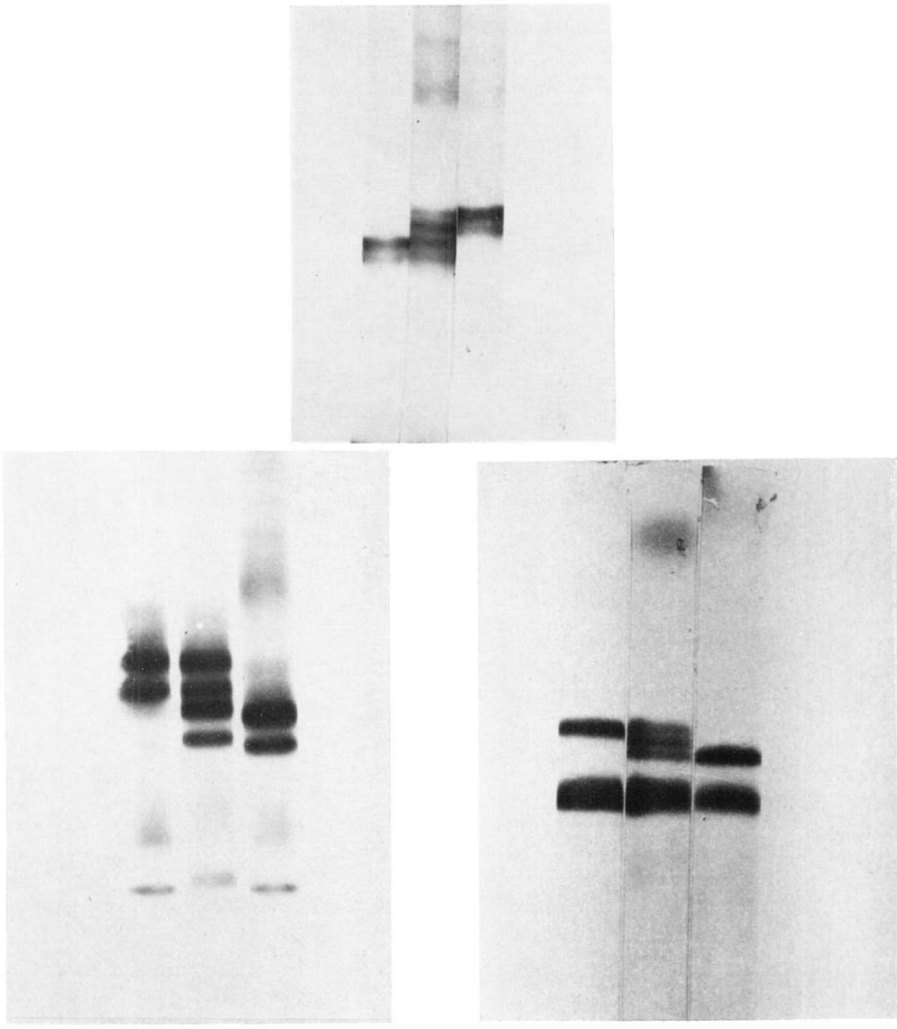

FIGURE 1.—a Electrophoretic phenotypes of malic dehydrogenase.
b Electrophoretic phenotypes of esterase.
c Electrophoretic phenotypes of alkaline phosphatase. The upper system is monomorphic while the more anodally migrating system is polymorphic.

isolated in tubes until they had released their progeny. The parental MDH genotypes were determined and only the offspring of heterozygous females were reared to maturity and then individually scored for their electrophoretic phenotypes. In a similar experiment, heterozygous females were crowded to cause the production of male offspring and these males were analyzed for their MDH genotypes. The results of these experiments and similar ones performed using females heterozygous for the other two systems are presented in Table 2. No evidence of recombination during parthenogenetic reproduction was detected as in each case all the progeny were heterozygous for the enzyme variant investigated.

TABLE 2

Parthenogenetic reproduction

Enzyme	Maternal phenotype	Number of mothers	Sex of progeny	Progeny phenotype
Malic	M/F	40	♀	144 M/F
Dehydrogenase		48	♂	120 M/F
Alkaline	S/F	15	♀	96 S/F
Phosphatase		27	♂	72 S/F
Esterase	S/F	34	♀	120 S/F
		22	♂	60 S/F

The genetic data presented here suggest that recombination does not occur during parthenogenesis. The conflicting view suggested by BACCI *et al.* (1961) rests entirely upon their supposition that chromosome pairing during parthenogenetic oogenesis will be accompanied by crossing over. This suggestion is unwarranted as crossing over is often absent despite normal meiotic behaviour, as it is for example in male Drosophila. It is concluded that recombination does not occur during parthenogenesis and as a result parthenogenetic offspring will be genotypically identical to their mothers.

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