Specialia

Table 2. Chain lengths of piscine muscle glycogens

| Source fish                      | Cardiac mus                 | cle                              |                                  | Red muscle                | ;                          |                                | White muscle                       |   |                                |  |
|----------------------------------|-----------------------------|----------------------------------|----------------------------------|---------------------------|----------------------------|--------------------------------|------------------------------------|---|--------------------------------|--|
|                                  | Total<br>unit               | External<br>branch<br>unit       | Internal<br>branch<br>unit       | Total<br>unit             | External<br>branch<br>unit | Internal<br>branch<br>unit     | Total<br>unit                      | External<br>branch<br>unit  | Internal<br>branch<br>unit     |  |
| Catla catla<br>Clarias batrachus | 10.57 ± 0.07<br>9.37 ± 0.15 | $8.3 \pm 0.10$<br>$7.8 \pm 0.21$ | $2.27 \pm 0.07 \\ 1.57 \pm 0.07$ | 10.5 ± 0.11<br>9.3 ± 0.09 |                            | $2.32 \pm 0.08$ $1.6 \pm 0.13$ | $12.52 \pm 0.11 \\ 11.12 \pm 0.20$ | $   \begin{array}{c}     10.1 \pm 0.11 \\     9.57 \pm 0.08   \end{array} $ | $2.42 \pm 0.07$ $1.5 \pm 0.10$ |  |

Values are  $\bar{x} \pm SE$  of 4 observations.

tissue from 10 freshly killed riverine carp Catla catla (1-1.5 kg) and 10 catfish Clarias batrachus (300-350 g). Glycogen was extracted and purified from pulvarized muscles according to Kjólberg et al.<sup>5</sup> and Somogyi<sup>6</sup>. Glycogen chain lengths were investigated by Kjólberg et al.<sup>5</sup> and Sayre et al.<sup>7</sup>.

White lateral muscles of both species have more glycogen than the red and cardiac muscles. The content does not vary in red and cardiac muscles (table 1).

In general, the muscle glycogens of Catla catla have greater chain lengths than those of Clarias batrachus (table 2). In an individual species, the red and cardiac muscle glycogens resemble each other in chain lengths (table 2). The length of internal branch unit of glycogens of conspecifics remains the same. White muscles of both species are characterized by having one glucosidal unit more in their external branches (table 2).

The results obviously support the view of Lawrie et al.<sup>3</sup> and show that the molecular species of glycogen reflect the functional aspects of metabolic specializations, since the cardiac and red muscles are geared to oxidative metabolism and the white muscles are anaerobic.<sup>8</sup> Another noteworthy observation is that the red and heart muscles of one species resemble each other in glycogen concentration and structural aspects of glycogen. Probably these muscles are not differentiated further than that of white muscles embryoni-

cally<sup>9</sup>. Unlike the mammalian glycogens, the fish muscle glycogens<sup>10,11</sup> of the present study show a constant internal chain length. The little variation in the degree of branching in different species of fish could be discernible from their genetic characteristics.

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## Genetic variation in natural populations: Morphological traits in *Drosophila melanogaster*<sup>1</sup>

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Summary. In a wild population of Drosophila melanogaster located near Madrid (Spain), it has been found that the frequency of morphological mutant phenotypes is 0.36 per captured female. The study of these females shows that they carry 3.6 recessive mutants in heterozygous condition per female. The genetic variability found is higher than the frequencies observed by other authors in other natural populations.

The evolutionary potential of a population is measured by the amount of genetic variation in the population: The more genetic variation there is, the greater the opportunity for evolution to occur<sup>2</sup>. Evolutionary geneticists have, therefore, attempted to ascertain levels of genetic variation in natural populations. Early studies of genetic variation investigated variants with morphological effects<sup>3-8</sup>. The discovery of the giant polytene chromosomes of Diptera later made possible the investigation of natural variation for chromosomal inversions<sup>9</sup>. More recently, the techniques of gel-electrophoresis have provided a wealth of data concerning polymorphisms in enzymes and other proteins<sup>10</sup>

However, the increase in knowledge brought about by the new methods has not been accompanied by additional research using the old, complementary methods of investigating genetic variation. In particular, the last 3 decades have seen the publication of few systematic studies of genetically determined morphological variation<sup>8</sup>. Yet, different kinds of variation are uncovered by morphological studies rather than by electrophoretic or other methods of

investigation. This is particularly relevant to the issue whether the variation is adaptatively significant – it has been questioned whether enzyme variation has any adaptive relevance, while many morphological traits are clearly adaptive. This paper reports a study of morphological variation in 3 samples of a natural population of *Drosophila melanogaster*.

Material and methods. The collections of Drosophila melanogaster flies were made in a small (387 × 13 m) isolated forest near Vallecas on the outskirts of Madrid. The forest, in the centre of the Spanish plateau, is characterized by typical continental climate and contains several Drosophila species that oscillate in relative abundance depending on the season<sup>11</sup>; melanogaster flies do not appear in the samples between November and April, but become extremely abundant in the summer months, with peaks between July and August.

2 sets of data are obtained for each sample: a) detectable morphological variation in the wild-collected females; b) variants manifested in inbred  $F_2$  progenies. 7 separate brother-sister matings were made with the  $F_1$  progeny of

Table 1. Number of females with a given number of mutant phenotypes in 3 samples from a natural population of Drosophila melano-

| Sample | Females  | Numbe | er of mutan | t phenotyp | es  | Total number | Mutations  |  |  |
|--------|----------|-------|-------------|------------|-----|--------------|------------|--|--|
|        | examined | 0     | 1           | 2          | 3   | of mutations | per female |  |  |
| A      | 222      | 166   | 50          | 5          | 1   | 63           | 0.28       |  |  |
| В      | 59       | 39    | 20          | _          | - , | 20           | 0.34       |  |  |
| C      | 87       | 44    | 37          | 5          | 1   | - 50         | 0.57       |  |  |
| Total  | 368      | 249   | 107         | 10         | 2   | 133          | 0.361      |  |  |

The sampling dates are: A, October 1970; B, June 1972; C, July 1972.

Table 2. Number of females with a given number of morphological recessive mutants in 3 samples from a natural population of Drosophila melanogaster

|       | Females  | Nu | Number of mutants |    |    |    |   |    |   |    |   |    | Total number | Mutations    | $\varkappa^2$ | р     |     |
|-------|----------|----|-------------------|----|----|----|---|----|---|----|---|----|--------------|--------------|---------------|-------|-----|
|       | examined | 0  | 1                 | 2  | 3  | 4  | 5 | 6  | 7 | 8  | 9 | 10 | 11           | of mutations | per female    |       | •   |
| A     | 40       | 2  | 5                 | 14 | 8  | 7  | - | 2  | 2 | -  |   | _  |              | 111          | 2.8           | 9.73  | 0.2 |
| В     | 30       | _  | 1                 | _  | 8  | 1  | 6 | 5  | 5 | 1  | 2 | _  | 1            | 161          | 5.4           | 14.51 | 0.1 |
| C     | 22       | _  | 2                 | 5  | 4  | 2  | 2 | 4  | 2 | .1 | _ | -  | _            | 88           | 4.0           | 5.61  | 0.5 |
| Total | 92       | 2  | 8                 | 19 | 20 | 10 | 8 | 11 | 9 | 2  | 2 | _  | 1            | 360          | 3.91          | _     | _   |

Sampling dates as in table 1. The agreement distributions between the observed and those expected from a Poisson distribution is tested with a chi-square.

each wild female; the progenies (F<sub>2</sub>) of the brother-sister mating were examined for the presence of mutant phenotypes. About 90% of all recessive alleles present in wild females are discovered with this method<sup>6</sup>.

Results and discussion. Only variants ascertained as having a genetic basis are included in the results. The mutations observed are those typically found in *Drosophila melanogaster* and are listed elsewhere<sup>12</sup>. The results of the first study, i.e. detectable morphological variation in the wildcollected females, are shown in table 1; since those results are variants directly observed in wild flies, they are either dominant mutants, or recessive in homozygous condition. The observed numbers of mutant phenotypes per female are 0.28, 0.34 and 0.57, respectively, in samples, A, B and C. These values are considerably higher than those observed by others authors in other natural populations of D. melanogaster. In an extensive study, Boesiger<sup>8</sup> observed a mean of 0.053 (range, 0.03-0.08) females with aberrant phenotypes in 3 populations, while Dubinin et al. 5 observed 0.087 and Berg<sup>13</sup> 0.068 individuals with mutant phenotypes; the incidence of mutant phenotypes is about 5 times larger (0.382 per female, on the average) in the Vallecas populations.

The 2nd study, i.e. variants manifested in inbred F<sub>2</sub> progenies, was designed to uncover recessive alleles in heterozygous condition. The results are summarized in table 2. The average number of recessive mutants detected per female is 2.8, 5.4 and 4.0 for samples A, B and C, respectively. The distribution of mutants among the females is random: the expectations derived from a Poisson distribution are not significantly different from the observed values. The number of recessive mutants found in the Vallecas population is also greater than the number observed by other authors: In D. melanogaster, Boesiger<sup>8</sup> observed a mean of 3.31 per female, while Spencer<sup>7</sup> observed 1.0 in D. mulleri and Alexander<sup>14,15</sup> 0.28 in *D. novamexicana* and 1.19 in *D. hydei*. It is difficult to know why the Vallecas population posesses such a wealth of morphological mutants. It is a relatively small population (probably smaller than the smallest population studied by Boesiger8), which must pass through narrow population bottlenecks during the winter months; moreover it is isolated from other populations of D. melanogaster, and therefore migration must be minimal. But small population size increases the probability of homozygosis, and thus leads to low frequencies of deleterious recessive mutants.

What are the processes maintaining the recessive morphological mutants observed in the Vallecas population? Are the frequencies observed consistent with a mutation-selection equilibrium? If we pool the data in table 2, we obtain 360 mutants in 92 females or 3.91 mutants per female. If selection is operating against a completely recessive deleterious mutant, the expected equilibrium frequency of the mutant is  $\hat{q} = \sqrt{u/s}$ , where u is the mutation rate per generation, and s the selective coefficient against the recessive homozygotes. The total number of gene loci in Drosophila may be around 5000. If we assume that there are 1000 loci at which morphological mutants can be observed, we obtain mutant frequency locus per  $q = 3.91/1000 \approx 0.004$ . A typical mutation rate for recessive alleles may be  $10^{-5}$  in *Drosophila*<sup>9</sup>. Since  $\hat{q} = \sqrt{u/s}$ , we have 0.000016s = 0.00001, or s = 1/1.6 = 0.63, which may not be an unreasonable selective coefficient against individuals homozygous for morpholocial mutants of the kinds observed in this study. If we assume that the total number of loci with morphological mutants is 500, then  $s \approx 0.15$ . It would seem that the frequencies of recessive morphological mutants observed in the Vallecas populations, although higher than the frequencies previously observed in other natural populations, may be explained as the result of an equilibrium between mutation and selection against the homozygotes, without postulating heterozygous advantage or any other mode of balancing selection.

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