

MORPHOLOGICAL DIFFERENCES BETWEEN TWO SIBLING SPECIES, DROSOPHILA PSEUDOOBSCURA AND DROSOPHILA PERSIMILIS

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The work on the population genetics of the sibling species, *Drosophila pseudoobscura* Frolova and *Drosophila persimilis* Dobzhansky and Epling has long been handicapped by the impossibility of distinguishing single individuals of these species by any morphological trait, and the consequent necessity of making cytological examinations or genetical tests. Lancefield¹ first differentiated these forms as "races or physiological species" on the basis of their genetic behavior, and called them "race A" and "race B" of *D. obscura* Fallen. Frolova and Astaurov² showed that Lancefield's "race A" from western United States differs from the European *D. obscura* in chromosome complement and in genital structure, and proposed for the former the name *D. pseudoobscura* Frolova. Because of the effectively complete reproductive isolation between "race A" and "race B," Dobzhansky and Epling³ recognized the latter as a separate species, *D. persimilis*. Mather and Dobzhansky,⁴ Reed, Williams and Chadwick⁵ and Reed and Reed⁶ made a statistical comparison of certain morphological characters in *D. pseudoobscura* and *D. persimilis*. Some average differences were found, but the overlapping of the variation curves proved so great that these differences were of no practical significance in recognition of the species.

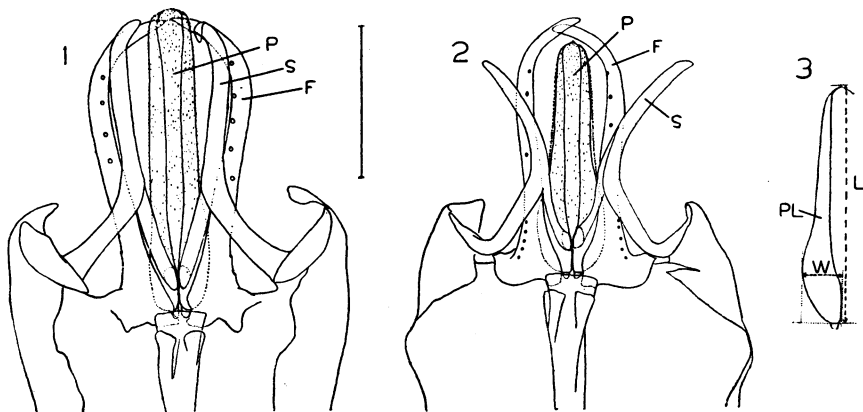
At the suggestion of Professors E. Mayr and Th. Dobzhansky, the writer undertook a detailed comparison of the male genitalia of the two species. Ten strains of *D. pseudoobscura* and ten of *D. persimilis*, derived from flies collected in various parts of the geographic distributions of each species, were used. All stocks were maintained at 16°C. The male flies were macerated in a 10% solution of KOH, washed in water, the genitalia removed, stained with carbol fuchsin and mounted in glycerin. Ten measurements from each strain were made with the aid of an ocular micrometer, one unit of which is equal to 0.0042 mm.

The structure of the genital arch and the hypandrium in the two species has been found to be alike. A clear-cut difference has, however, been noted in the dimensions and the proportions of the penis (Figs. 1 and 2). A description of the morphology and homologies of various parts of *Drosophila* male genitalia has been given by Salles.⁷

The penis of *D. pseudoobscura* is relatively long and cylindrical, whereas that of *D. persimilis* is shorter and broader at its base with a tapering appearance. The length of the penis is measured from the base of its lamina,

excluding the articular condyle, to the distal end of the lamina. Care was taken not to rupture the membrane at the tip of the penis. The width was measured at the greatest curvature of the penis' lamina with respect to the mid antero-posterior axis of the penis (Fig. 3). The penis index is computed as the ratio: length of the penis/width of lamina. The results of the measurements are summarized in table 1.

There is no significant difference among the geographical strains of *D. pseudoobscura*, nor among the strains of *D. persimilis*. However, the difference in the index of the two species is highly significant. The mean index for *D. pseudoobscura* is 8.61 ± 0.31 ; the mean index for *D. persimilis* is 6.48 ± 0.51 . Considering the extremes in the two species, we may conclude that any individual with a penis index equal to or above 7.64 is



FIGURES 1 AND 2. Camera lucida drawings of the penis and accessory parts in *Drosophila pseudoobscura* and *D. persimilis*, respectively: *F*, forcep; *P*, penis; *S*, stylus. FIGURE 3. The measurements taken on the lamina of the penis: *L*, length; *PL*, penis lamina; *W*, width. The scale represents 100 micra.

pseudoobscura; a penis index equal to or below 7.60 indicates *persimilis*. One *pseudoobscura* male out of 100 measurements had an index 7.64. This extreme was obtained from different absolute units than the 7.60 index of *persimilis*. Considering this situation, we should employ both criteria for classification. On the basis of the shape of the penis and also the index we are definitely able to identify males of the two species.

The question that now arises is whether such morphological differences as those described are of any value in understanding sexual isolation between the species. Mayr⁸ believes that some functional difficulties are encountered in heterospecific matings such that "incomplete copulation" is the result. Our findings show definite differences in the size and shape of the penis of the two species; however, we can not assign the functional

difficulties to this structure alone. In addition, as indicated by the points of articulations, the styli have a functional relation with the penis. It seems hopeful that further studies on the mechanism of the genitalia of *D. persimilis* and *D. pseudoobscura* may reveal some coordinated movements of various parts constituting a specific sequence which may differ in the two species.

TABLE 1
MEASUREMENTS AND PENIS INDICES OF DIFFERENT STRAINS OF *D. Persimilis* AND *D. Pseudoobscura*

STRAIN	MEAN LENGTH	MEAN WIDTH	INDEX	
			MEAN	LIMITS
<i>Pseudoobscura</i>				
Atitlan, Guatemala	42.9	5.00	8.58 ± 0.057	8.20-8.80
Chichicastenango, Guatemala	44.5	5.00	8.90 ± 0.035	8.80-9.00
Amecameca, Mexico	43.2	5.00	8.64 ± 0.057	8.40-9.00
Cuernavaca, Mexico	43.6	4.95	8.82 ± 0.120	8.60-9.78
Black Mesa, Arizona	42.1	4.95	8.51 ± 0.066	8.20-8.89
Coffee Creek, California	41.3	5.05	8.18 ± 0.095	7.64-8.60
Alturas, California	44.2	5.15	8.59 ± 0.089	8.18-9.00
Zion, Utah	42.5	5.00	8.50 ± 0.054	8.20-8.80
Aspen, Colorado	42.5	4.95	8.59 ± 0.082	8.20-9.11
Mara, British Columbia	44.6	5.00	8.92 ± 0.066	8.60-9.20
<i>Persimilis</i>				
Aspen Valley, California	37.9	6.00	6.32 ± 0.029	6.17-6.50
Coffee Creek, California	39.2	6.70	5.91 ± 0.123	5.57-6.13
Deer Creek, California	38.5	6.45	5.91 ± 0.146	5.43-6.50
Nahogui, California	38.6	5.65	6.85 ± 0.114	6.33-7.40
Orick, California	36.9	5.90	6.28 ± 0.136	5.83-7.20
Porcupine Flat, California	37.3	5.45	6.85 ± 0.041	6.73-7.20
St. Helena, California	37.7	5.35	7.06 ± 0.123	6.55-7.60
Sequoia Park, California	38.5	5.85	6.59 ± 0.086	6.33-7.09
Hope, British Columbia	37.5	5.65	6.67 ± 0.165	6.00-7.60
Quesnell, British Columbia	38.4	6.00	6.40 ± 0.117	6.17-6.50
Mean penis index for <i>D. pseudoobscura</i>			8.61 ± 0.03	
Mean penis index for <i>D. persimilis</i>			6.48 ± 0.05	

NOTE: Mean length and mean width are in ocular units. The mean penis index of each strain is given with its standard error.

Summary.—Because of a complete reproductive isolation, *Drosophila pseudoobscura* and *D. persimilis* are considered separate species. However, no morphological differences between them were known. It is shown that the males of these sibling species can easily be distinguished by the shape of their genitalia.

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⁶ Reed, S. C., and Reed, E. W., *Evolution*, **2**, 40-48 (1948).

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A CONDITION FOR A REAL LATTICE TO DEFINE A ZETA FUNCTION

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In Theorem 1 we shall prove the following: If the product of n linear forms in n variables, whose coefficients are real and whose determinant is positive, assumes only a finite number of different values in a finite interval, and assumes the value 0 only if all the variables are 0, then one of the linear forms arises from a ring in an algebraic number field, and the other $n - 1$ linear forms are the $n - 1$ different conjugates of the first linear form. Hence, the product is essentially the norm of all numbers in an order of an algebraic number field, which clearly takes on only a finite number of values in any finite interval.

This problem arose in connection with a forthcoming paper of S. Bochner,¹ "Some Properties of Modular Relations." We show that if any real lattice gives rise to a zeta function, the lattice comes from an order in an algebraic number field.² One can expand this to prove that the zeta function will satisfy a certain functional equation.³ To define a zeta function from any real lattice it is clear that one must have certain properties of discreteness on the product of the forms to insure convergence. However, in the proof of Theorem 1, discreteness of the product is needed for only a finite interval. We thank Professor Bochner for letting us see in advance a copy of his paper.

Definition: Let x_i be real linear forms in u_j , i.e.,

$$x^{(i)} = u_1 w_1^{(i)} + u_2 w_2^{(i)} + \dots + u_n w_n^{(i)} \quad [i = 1, 2, \dots, n], \quad (1)$$

where $w_j^{(i)}$ is real and the determinant $\Delta = |w_i^{(j)}|$ is positive.

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