

6. The relationships between the different electrode leads, by which steady potentials can be measured in association with 30° lateral fixations, appear to be quite constant in normal subjects. The equation: $Ld. 1 + Ld. 2 = Ld. 3 + Ld. 4$ was found to hold closely in the averages for each sub-group on each day. There is, however, a consistent tendency for $Ld. 3 + Ld. 4$ to be a little higher than expected. All comparisons thus far worked out show this tendency which averages +3 per cent. The fact that Lead 3 was the first measurement in the series for each patient on each day may have a bearing on the results.

7. A consistent tendency was found for the steady potential measurements to show a slightly smaller value on the second than for the first day. It is assumed that this change rests on psychological factors of mental attitude and adjustment to the laboratory procedure. This is a significant finding, pointing as it does to a relationship between the strength of the eye's steady potential and the psychological state of subjects cooperating in the experimental routine.

* The expenses of this investigation were met in part by a grant from the Knight Fund of Yale University School of Medicine.

† In the previous paper it was suggested that Lead 3 represents the optimal steady potential average for the two eyes. It now appears also to be the most dependable of the several measures of potential used in these studies.

¹ W. R. Miles, "Performance of the Einthoven Galvanometer with Input through a Vacuum Tube Microvoltmeter," *Jour. Exper. Psychol.* (in press).

² W. R. Miles, "The Steady Polarity Potential of the Human Eye," *Proc. Nat. Acad. Sci.*, 25, 25-36 (1939).

ON THE SUBDIVISION OF THE GENUS *DROSOPHILA*

BY A. H. STURTEVANT

W. G. KERCKHOFF LABORATORIES OF THE BIOLOGICAL SCIENCES, CALIFORNIA INSTITUTE OF TECHNOLOGY

Communicated January 28, 1939

There is now in progress in several laboratories a comparative study of the genetics of the species of *Drosophila*. Several authors have pointed out possible deductions concerning the history of the group that may be derived from such studies (e.g., Donald 1936, Sturtevant and Tan 1936, Serebrovsky 1938). If such deductions are to be of value, it is desirable that there be available a satisfactory arrangement of the species into some scheme of classification that can be taken as indicating their degree of genetic relationship. It is the purpose of this note to present the results

of an attempt to derive a classification by a method as free of personal equation as it can be made.

There are forty-two species of *Drosophila* in culture in this laboratory, and these have all been examined for a series of twenty-seven different characters. These characters, which concern the eggs, larvae, pupae and imagines, and include both structural characters and those having to do with the habits of the animals, are all that have so far been worked out that satisfy the following requirements:

(a) Each of the species must be capable of classification for every character. Some characters, such as presence or absence of clouds on the cross-veins, permit of a classification into two groups, one having the character, the other lacking it. Other characters, such as proportions of the sections of wing-veins, or number of branches of anterior pupal spiracles, are numerical. In such cases an arbitrary amount of difference between two species was set as being significant.

(b) There must be at least two species in each category concerned—i.e., a character occurring in only one of the available species was not included.

(c) Two characters obviously likely to be developmentally closely related, or likely to be affected similarly by natural selection, were not both included. This requirement is difficult to apply, and does admit a large element of personal judgment. The rule here should be to include no doubtful cases.

Having a table showing the condition of all 27 characters in each of the 42 species, two different types of analysis were then carried out. A table was made showing, for each species, the number of characters in which it differed from each of the other 41. This table may be taken as giving a first approximation to the degree of genetic difference between any two species—and therefore to their remoteness of genetic relationship. The accuracy of this index evidently depends on several factors, but it seems legitimate to conclude that most resemblances are due to likeness of genetic constitution, and that separate origins of similar constitutions are not likely to give parallel resemblances in many different characters.

Each of the 27 characters was then compared with each of the others, to determine if the distribution of the two was correlated. Here a striking result was at once evident; there is a single group of correlated characters that splits the available species into two groups, with a few forms having combinations of characters that disagree with the usual correlations. Reference to the species-by-species table shows that all but one of these anomalous types can be connected, through a series showing as few as six differences between successive species, to one or the other of the major groups. *Drosophila duncani* alone fails to show such a series of connections, since it differs from every one of the remaining species by at least nine characters. If the remaining species are separated into two groups,

study of the table shows that the minimum number of differences between two species belonging to different groups is also nine.

The following classification is therefore indicated:

Subgenus *Dasydrosophila* Duda

Ventral receptacle not finely coiled; posterior pair of Malpighian tubes fused to form a ring around the gut; four blunt filaments on the eggs; dark bands on posterior margins of second to fifth abdominal segments not thinner or broken in median dorsal line.

Species: *D. duncani* Sturtevant (Illinois, Ohio).

Subgenus *Drosophila* Fallén

Ventral receptacle finely coiled, resembling a more or less tangled spring; posterior pair of Malpighian tubes fused; three or four tapering filaments on the eggs; dark posterior bands of at least the two basal abdominal segments thinner or broken in median dorsal line.

Species agreeing in all these characters: *D. funebris* Fabricius (type—temperate regions); undescribed species near *funebris* (Texas); *D. guttifera* Walker (southeastern United States); *D. hydei* Sturtevant (American); four undescribed species near *repleta* and *hydei* (Mexico, Guatemala, California); *D. repleta* Wollaston (cosmopolitan); *D. mulleri* Sturtevant (American); *D. immigrans* Sturtevant (cosmopolitan); *D. tripunctata* Loew (southeastern United States) *D. testacea* v. Roser (north temperate zone); *D. busckii* Coquiller (cosmopolitan).

Species diverging in one or more of the characters listed:

Posterior Malpighian tubes apposed, but not with continuous lumen: *D. cardini* Sturtevant (tropical America); *D. robusta* Sturtevant (eastern United States).

Egg filaments blunt: *D. virilis* Sturtevant (Japan, China—rare in the United States).

Egg filaments two, blunt: *D. melanica* Sturtevant and two related species (eastern United States). In one of the undescribed species the ventral receptacle is not finely coiled. Were it not for its close resemblance to *melanica* and to *mulleri* the position of this species would be doubtful.

Subgenus *Sophophora*, subg. nov.

Ventral receptacle not finely coiled; posterior pair of Malpighian tubes free, not united at their apices; eggs with two blunt filaments; dark posterior bands of second to fifth abdominal segments broader in median dorsal line, or of uniform width.

Species agreeing in all these characters: *D. melanogaster* Meigen¹ (type—cosmopolitan); *D. affinis* Sturtevant (eastern United States); *D. algonquin* Sturtevant and Dobzhansky (eastern North America); *D. alhabasca* Sturtevant and Dobzhansky (northern North America); *D. azteca* Sturtevant and Dobzhansky (California to Guatemala); *D. narragansett* Sturtevant and Dobzhansky (eastern United States); *D. psuedo-obscura* Frolowa (western North America); *D. subobscura* Collin (Europe); *D. miranda* Dobzhansky (western United States); *D. ananassae* Doleschall (Tropics, old and new worlds); *D. bipectinata* Duda (tropical Asia); *D. auraria* Peng (China, Japan); *D. simulans* Sturtevant (cosmopolitan); *D. takahashii* Sturtevant (Formosa, China); *D. willistoni* Sturtevant (American tropics); six species (probably all undescribed) related to *D. saltans* Sturtevant (Mexico and Central America).

Less complete analysis suggests the following distribution for certain species not now in cultivation in this laboratory:

Subgenus *Drosophila*: *D. quinaria* Loew, *D. transversa* Fallén, *D. similis* Williston, *D. latevittata* Malloch, *D. californica* Sturtevant, *D. komaii* Kikkawa and Peng, *D. bizonata* Kikkawa and Peng.

Subgenus *Sophophora*: *D. nebulosa* Sturtevant, *D. obscura* Fallén, *D. seminole* Sturtevant and Dobzhansky, *D. montium* deMeijere, *D. lutea* Kikkawa and Peng.

As indicated, one of the three subgenera has already been recognized by Duda (1925), who has established several subgenera. Two others of these are represented among the species here considered: *Acrodrosophila* Duda is based on *D. testacea*, and *Spinulophila* Duda (= *Acanthophila* Duda) includes *D. immigrans*. Each of these subgenera was based on a single character, and the present analysis does not indicate that the species concerned are particularly out of place in the typical subgenus. *Dasydrosophila* was based on several characters, the following being a translation of the diagnosis: Third antennal segment very large, at least twice as long as broad and two to three times as long as the second segment, often long haired; facial carina usually low, only exceptionally nose-like; arista with only a single branch below basal to the terminal fork. (In *D. duncani* there are two such branches of the arista.) The type-species is from the Oriental region, and Duda also refers several tropical American forms to this group. I have examined no others for the series of characters here utilized, but it may be supposed that the species associated by the characters given by Duda constitute a natural group.

Unfortunately the distinction between the other two subgenera is not easily made with ordinary museum material. Of the characters given, only the abdominal banding is evident in pinned specimens—and this is often obscured by shrinkage. Other characters may be helpful, as follows: Sex-combs on the male tarsi occur only in *Sophophora*; species

appreciably larger than *melanogaster* are found only in *Drosophila*; the "costal index" (length of second section of costa divided by length of third section) averages lower in *Sophophora* (range from 1.2 to 3.1) than in *Drosophila* (2.8 to 4.3, with *D. guttifera* at 2.0); the "sterno-index" (length of anterior sternopleural bristle divided by length of posterior—Kikkawa and Peng 1938) averages lower in *Sophophora* (0.3 to 0.6) than in *Drosophila* (0.5 to 0.9, with *D. busckii* at 0.3 and *D. guttifera* at 0.4).

The present account is not to be considered as a final one. Several of the characters used are unsatisfactory, and others are not yet measured accurately. It is hoped that, with improved classification of these and with the utilization of more characters, the method may be extended to indicate still finer subdivisions of the genus. It is also probable that additional species will be studied, and these may require some modifications of the scheme here outlined—though partial analysis of several aberrant types has, so far, suggested that such modifications will consist chiefly in the addition of new subgenera, rather than in the rearrangement of the species here considered.

¹ This is the species known to all geneticists under this name (synonym, *D. ampelophila* Loew). Some authors now use the name *D. fasciata* Meigen. There is some reason for this substitution; but I am not convinced that the argument for it is conclusive. In any case there is no other species to which the name *melanogaster* is properly applicable; and with so widely known and unambiguous a name I am convinced that too close adherence to the strict rules of taxonomy is only pedantic and confusing.

Donald, H. P., *Jour. Genet.*, **33**, 103-122 (1936).

Duda, O., *Arch. Naturgesch.*, **91A**, 11-12, 1-229 (1925).

Kikkawa, H., and Peng., R. T., *Japan. Jour. Zool.*, **7**, 507-552 (1938).

Serebrovsky, A. S., *C. R. Acad. Sci. U. S. S. R.*, **19**, 77-81 (1938).

Sturtevant, A. H., and Tan, C. C., *Jour. Genet.*, **34**, 415-432 (1936).

EMBRYO-SAC DEVELOPMENT IN PLUMBAGELLA

By J. W. BOYES¹

DEPARTMENT OF BOTANY, UNIVERSITY OF WISCONSIN

Communicated January 23, 1939

Dahlgren² in 1916 reported on the development of the embryo sac in the Plumbaginaceae. Throughout the family the primary archesporial cell gives rise to a parietal cell and a macrospore mother cell, the latter of which functions as an embryo-sac mother cell. In the sub-family Plumbagineae, of the four nuclei formed by the meiotic divisions two lie at one end of the embryo sac separated from the two at the other end by a large