

Fig. 2. Relation between percentage of flowers without anthers and solar radiation 17 days before anthesis. Solar radiation was measured as calories per square centimeter per day. The coefficient of correlation $r = .50$, significant at the .01 level of probability.

of only minor importance in the development of c.p. flowers. The highly significant correlations with temperature which were observed with male-sterile flowers and with the External Ovule abnormality (4) were not obtained for c.p. flowers. Both the c.p. studies and the earlier research on cotton flower development show clearly that changes in the weather can bring about changes in flower structure.

The carpelloid petal flowers develop gymnosperm structure in response to hot, dry weather. Under cool, moist conditions they are likely to produce normal angiosperm flowers. Perhaps a sudden shift in climate caused many different kinds of gymnosperms to develop abnormal flowers. A gymnosperm which had evolved a "flower" structure adapted to vector pollination might well have a central ring or cone of megasporophylls. A change in growth rate could delay separation of the ring of tissue into separate carpel primordia and cause the fusion of some or all of the carpels. Climatic change after some gymnosperms had already begun genetic evolution to accommodate different pollen vectors, and different ecological niches could produce a similar developmental change in many separated groups from a common origin without requiring any simultaneous genetic mutations. The result would be a sudden development of angiosperms over a wide area from groups already morphologically distinct.

The carpelloid petal flowers suggest that gene repression may be a very important aspect of flower development. The same c.p. abnormality has occurred in other stocks derived from crosses with *Gossypium anomalum* cytoplasm; this would indicate that the abnormality is not due to a new gene mutation, but comes from expression of genes which are present at least in *G. anomalum*, but not usually expressed. All of the wild and cultivated cotton species have evolved control systems for flower development which result in a ring of bracts, a ring of calyx tissue, a ring of petals, and a tubular androecium surrounding a single style at the tip of a compound ovary. Interspecific hybrids make drastic changes in the controls. They introduce new combinations of genes into cytoplasm which evolved to fit other species growing in other places. Repressor genes get left out of new combinations. A cytoplasmic organelle may produce a 2-carbon side-chain where a 3-carbon one "ought" to be. The enzyme or hormone that is supposed to fit needs twice as long to get around to turning on the next set of genes.

The great variety of patterns of differentiation of c.p. flowers fits very well into Heslop-Harrison's concept (5) of a relay system of genes activated in an irreversible order, accompanied by inhibition (repression) of other genes. His requirement that competence for differentiation of sex organs be accompanied by loss of capacity for growth would apply to most of the flower organ abnormalities. In carpelloid petal plants part of each petal primordium would remain meristematic; the bud could switch to carpel production at any stage from outgrowth of petal primordia to the normal period for producing carpels and ovules. The fate of the primordia which normally develop into anthers would depend on both the

rate of development and the timing of the switch from petal to anther to carpel programming within any one flower bud. Probably androecial tissue which was not already committed to anther production when the bud's chemistry changed to "carpel mix" would simply produce carpels. Tissue started on the program for anther production would produce anthers or cease development according to how far it had gone in the program, or perhaps according to how strongly the new signals countermanded the old ones.

The genetic mechanisms responsible for flower abnormalities could fit either the structural-operator-regulator complexes required by the Jacob-Monod theory of gene activity (6) or the more complicated Britten-Davidson hypothesis derived from it (7). In either case, a small population of living plants may offer some suggestions about possible courses for evolving control of the gene action which results in the usual rigidly specified flower structure of angiosperms.

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"Sex Ratio" in *Drosophila pseudoobscura*: Spermiogenic Failure

Abstract. Contrary to earlier reports, testes of "sex ratio" *Drosophila pseudoobscura* males have only half as many sperm per bundle as testes of normal males do. This fact, determined from electron micrographs, indicates that the functional pole hypothesis is not applicable to the action of "sex ratio."

"Sex ratio" is a widespread genetic condition of the X chromosome in *Drosophila*. It was first described in detail for *D. obscura*, a European spe-

cies (1), and has since been studied in other members of the genus (2-4). During these studies it was observed that males carrying the "sex ratio" X

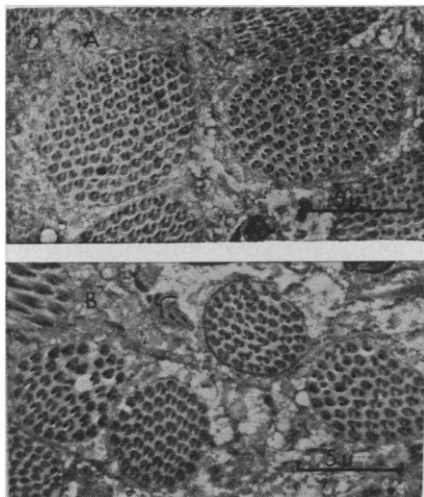


Fig. 1. (A) Electron micrograph of a section of a whole testis from a normal *D. pseudoobscura* male, showing cross sections of sperm bundles. (B) A section from a "sex ratio" male.

chromosome produced progeny consisting almost entirely of females because only X-bearing sperm function in fertilization; it was also reported that the full complement of 128 spermatids (2, 4) and sperm (4) per bundle was present. In addition, it was reported that the X chromosome divides twice at the first meiotic division (2), thus giving rise to the extra X-bearing sperm, but Novitski, Peacock, and Engle (4) were unable to find evidence of any abnormality of the X chromosome at meiosis. They explained the phenomenon of "sex ratio" on the basis of the regular nonfunctioning of meiotic products, as proposed for *D. melanogaster* (5). In the case of the "sex ratio," according to this hypothesis, the X chromosome is favored and the unisexual progeny can be explained by "preferential movement of the X chromosome to the functional pole at anaphase I" (4). We have been able to confirm the earlier reports that over 100 spermatids per bundle are present in "sex ratio" males (2, 4), but we find only about half that number of mature sperm per bundle. As a result of these findings, we suggest that the action of "sex ratio" cannot be explained on the basis of regular nonfunctioning of meiotic products, but rather should be described as spermiogenic failure.

For this study we used descendants of the flies collected by Novitski and Sturtevant (4), as well as male progeny of wild females recently collected near Tucson, Arizona. Whole testes of day-old males were fixed in 2

percent osmium tetroxide, embedded in Epon, and sectioned. Smear preparations of testes were also made for combined light and electron micrography (6) and fixed as above. Photographs of the smear preparations were taken with the light microscope perpendicular to the plane of sectioning both before and during the sectioning procedure. This permitted identification of the sections with respect to their position on the bundle as well as with respect to the size of the bundle. Some of the sections were photographed on a Philips EM-300 electron microscope and some on a Hitachi HS-7S.

The mean number of sperm per bundle as shown by electron micrographs of sectioned testes was 112 ± 7.4 (nine bundles) in normal males and 55 ± 8.2 (38 bundles) in "sex ratio" males (Fig. 1).

Three different sizes of sperm bundles have been reported as a regular feature of spermatogenesis in *D. pseudoobscura* (7). There was no difference in number of sperm per bundle in the three sizes. When using squashes stained with aceto-orcein and Feulgen stains we experienced great difficulty in counting mature sperm, and we feel that these light-microscopic methods are inadequate for the counting of sperm bundles in *D. pseudoobscura*.

Since "sex ratio" males have only half as many sperm per bundle as normal males, it seems reasonable to conclude that the action of "sex ratio"

does not depend on a functional pole. The problem arises of how "sex ratio" maintains a frequency as high as 30 percent in some populations (2) if "sex ratio" males produce only half as many sperm as normal. There is also laboratory evidence that "sex ratio" is selected against (3), which compounds the problem.

The population dynamics of "sex ratio" in nature is not understood, but, if females are not limited in their fecundity by the amount of sperm they receive, then "sex ratio" is probably a good example of a chromosome meiotically driven to a high frequency against adverse selection (8).

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Prolonged Learning and Split-Brain Cats

Abstract. *A definite relation is shown between interhemispheric transfer and speed of learning. Split-brain cats were trained in a variety of discriminations, and the success or failure of interhemispheric transfer was evaluated with regard to rate of learning. When interhemispheric transfer succeeds, learning time is normal; when interhemispheric transfer fails, learning time is prolonged, becoming at least twice that of normal. Retention is also poor in those animals that exhibit prolonged learning. A normal learning curve appears to be the product of interaction between both cerebral hemispheres during learning.*

Effects of hemispheric division on learning and memory are relatively unknown. Past experiments with "split-brain" cats and monkeys (1) and with cerebral deconnection in man (2) have helped to increase our understanding of the function of the corpus callosum and other midline structures in their role of transmitting sensory information from one hemisphere to the other. Little attention, however, has been given to

these same studies with regard to the contribution of each cerebral hemisphere to memory and the learning process.

I now report experiments in which interhemispheric transfer is compared with the speed of learning in normal animals and in split-brain animals prepared with a variety of commissurotomies as well as with cortical ablation. Retention is also compared