A GYNANDROMORPH SEGREGATING FOR AUTOSOMAL MUTANTS IN *DROSOPHILA SUBOBSCURA*

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(With Two Text-figures)

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Introduction

Gynandromorphs in *Drosophila* are interpreted as having arisen in three ways. Firstly, by the partial or total elimination of an X-chromosome during development. This, the most common type in *D. melanogaster*, has been monographed by Morgan & Bridges (1919), and by Patterson & Stone (1938). In *D. melanogaster* elimination of an X-chromosome occurs either spontaneously, or by experiment with the use of X-rays, or in the presence of the Minutes (Bridges, 1925*a*; Stern, 1936). Sturtevant (1929) has shown that the autosomal mutant *claret* produces large numbers of gynandromorphs in *D. simulans*. Secondly, sex mosaics have been shown to arise by haploidy, that is, by the loss of a whole set of parental chromosomes. In *D. melanogaster* Bridges (1925*b*) has described two haploid-diploid sex mosaics in which there was a loss of the maternal genome and also some reduction in the size of the haploid parts. In *D. pseudo-obscura* forty-five such mosaics, produced by the sex-linked dominant *Plexus*, were described by Crew & Lamy (1938). In all but one case the maternal set of chromosomes was lost from the haploid region. There was no apparent reduction in the size of the haploid regions. The third type, due to double fertilization, is the rarest. In *D. melanogaster* nine possible cases out of about 100 were reported by Morgan & Bridges (1919), and nine out of 335 by Patterson & Stone (1938). Crew & Lamy (1938) report three certain and one possible case out of forty-nine in *D. pseudo-obscura*. In *D. subobscura* Maynard Smith (1952) has described one case, previous to that reported here, of a gynandromorph produced by double fertilization.

Origin, structure and behaviour of the gynandromorph

From the paired mating $\frac{fs\ \ pp\ \ sj\ \ otp\ pl}{+\ \ +\ \ +\ \ +\ \ +}$ ♀ × $\frac{fs\ pp\ sj\ otp\ pl}{fs\ pp\ sj\ otp\ pl}$ ♂ involving the fourth chromosome autosomal mutants, *fs* (partial fusion of the third and fourth longitudinal wing veins), *pp* (bright red eye colour), *sj* (six-jointed tarsi), *otp* (outspread wings), and *pl* (a plexus of veins, especially between the second and third longitudinal veins), the gynandromorph illustrated in Fig. 1 was found.

The right wing shows the mutant *fs* (fused). The left wing shows instead *otp* (outspread) and *pl* (plexus). The posterior pair of legs show the mutant *sj* (six-jointed), whereas the fore and middle pairs are wild type. Both the eyes are wild type.

The gynandromorph was long lived (about 3 weeks) and many attempts were made to cross it to $\frac{fs\ pp\ sj\ otp\ pl}{fs\ pp\ sj\ otp\ pl}$ males, but in vain. Consequently its behaviour was studied.

When placed with females it made male-like reactions, that is, it, or rather he, flicked both his male and female wings in the typical male-like manner. He did not attempt to copulate. The gynandromorph died before its behaviour, when put with males, could be studied. It is not known if it was mated by the $\frac{fs\ pp\ sj\ otp\ pl}{fs\ pp\ sj\ otp\ pl}$ males. Males will court each

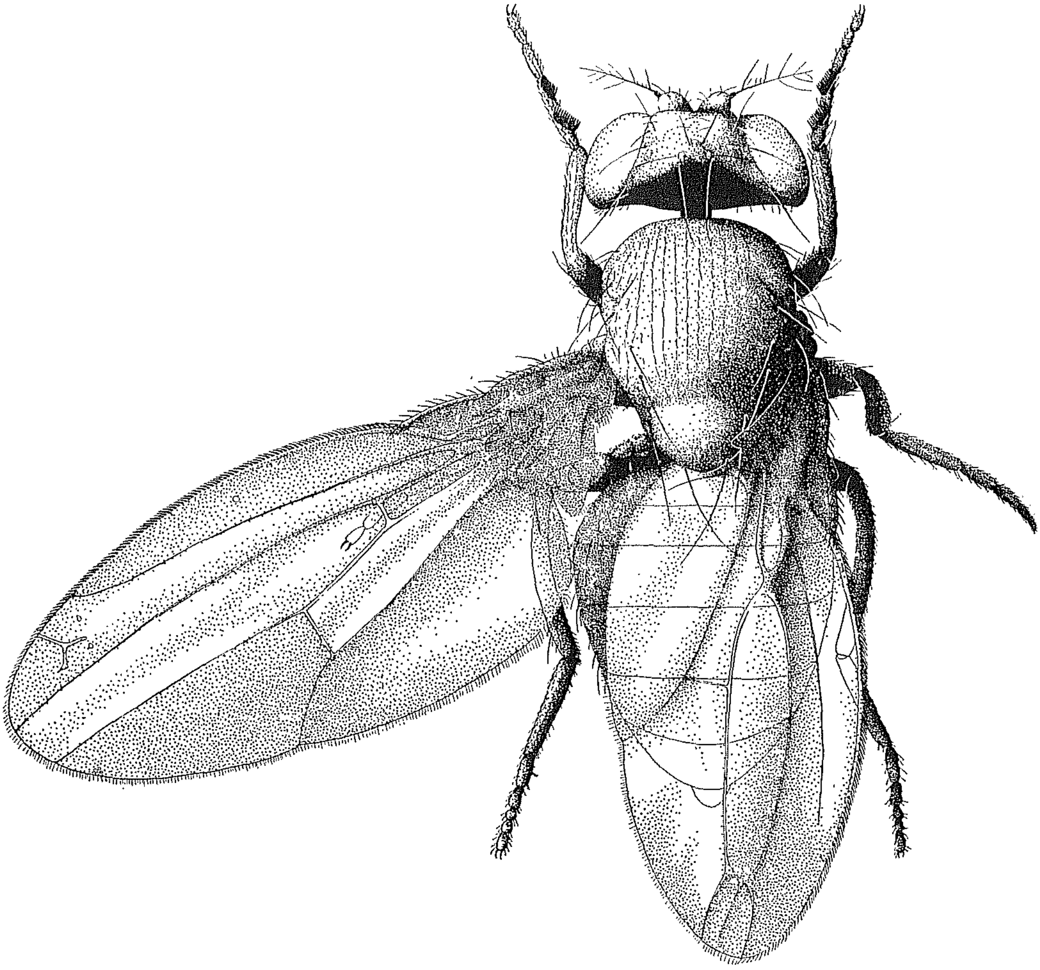

Fig. 1.

other but fail in their attempts to mate because the courted male chases the courting male away. Since the gynandromorph behaved like a male when with females, it may be assumed that it did so when with males.

The sex of the regions may be determined either directly or by inference. The forelegs bear sex combs which are typical male-like structures. The middle pair are wild type like the fore pair, and it may therefore be inferred that they are also of male tissue. The hind legs are inferred as being female. Since the gynandromorph showed typical male-like behaviour, it may be taken that the head or at least the brain is male. It will be noticed that the right wing is smaller than the left wing. This is interpreted as being the expression of the sexual dimorphism characteristic of *Drosophila*, the wings of males being proportionally smaller than those of females. The abdomen is female in shape and structure. The nature of the gonads has not been determined because to do so would ruin the specimen. But since no orange colour was seen through the body wall, testes are assumed to be absent and ovaries present.

Since it is not possible to distinguish between male and female cuticle the exact line of demarcation between male and female parts cannot be determined. This line lies somewhere between that region of the thorax to which male structures are attached (forelegs, head, and right wing) and that to which female structures are attached (abdomen, hind legs, and left wing). That is, approximately the anterior two-thirds of the thorax is of male tissue and the remaining third of female tissue. The line of demarcation passes somewhere obliquely across the thorax. It is therefore a 'fore-and-aft' gynandromorph of Morgan and Bridges, the commonest type in *D. subobscura* (Spurway, 1942).

DISCUSSION

This gynandromorph can be explained by assuming double fertilization by X- and Y-bearing sperm of the egg and second polar body nuclei, if one of these nuclei contained a *fs* + + + + chromosome and the other a + *pp sj otp pl* chromosome. It is suggested that the zygote formed by the union of the Y-bearing sperm and the nucleus containing the *fs* + + + + chromosome formed the anterior and male part of the insect, and that formed by the X-bearing sperm and the nucleus containing the + *pp sj otp pl* chromosome the posterior and female part. Since attempts to cross this gynandromorph with $\frac{fs\ pp\ sj\ otp\ pl}{fs\ pp\ sj\ otp\ pl}$ males failed, it was not possible to say whether or not *pp* was contained in the posterior part.

Sonnenblick (1950) in *D. melanogaster* and Fahmy (1952) in *D. subobscura* have shown that the spindles of the first and second meiotic divisons lie in tandem and perpendicular to the surface of the egg, and that the innermost of the four reduced nuclei normally becomes the egg pronucleus. The other three are described as disintegrating into the cytoplasm (Rabinowitz, 1941; Fahmy, 1952), that is, polar bodies are not extruded. This being so it is possible that the egg and second polar body nuclei could be fertilized and so produce the gynandromorph, provided that one of these nuclei contained a *fs* + + + + chromosome and the other a + *pp sj otp pl* chromosome. To have a meiotic process in which a *fs* + + + + and + *pp sj otp pl* chromosome go to each of the poles at the first meiotic anaphase involves four strand crossing-over between *fs* and *pp* (Fig. 2*a*). One alternative to four-strand crossing-over is three-strand crossing-over as illustrated in Fig. 2*b*. This would require that the upper pair of chromosomes, labelled (i) in this figure, go to the inner of the two poles at the first meiotic anaphase and subsequently pass to the two pronuclei which are to be fertilized.

The other alternative is that there is two-strand crossing-over, as illustrated in Fig. 2*c*, followed by fertilization of one product of each of the second meiotic divisions, i.e. nuclei containing the chromosomes labelled (ii) and (iii) in Fig. 2*c*. In these figures centromeres are omitted because it is not known at which end of the chromosome they lie. The chromosomes in *D. subobscura* are acrocentric.

Maynard Smith (1952) described a gynandromorph in *D. subobscura* segregating for autosomal mutants, but in this case it was not possible to say whether it was due to double fertilization of reduced egg pronuclei or of the first two cleavage nuclei. With the discovery of the present gynandromorph, the first possibility is suspected as being the more likely.

Crew & Lamy (1938) described mosaics in *D. pseudo-obscura*, some of which were due to double fertilization, but in no case were all the four pronuclei involved of different chromosomal constitution, as is the case in the mosaic illustrated here. So far as is known this is the first certain published case of a gynandromorph resulting from the union of two different egg nuclei with two different sperm nuclei.

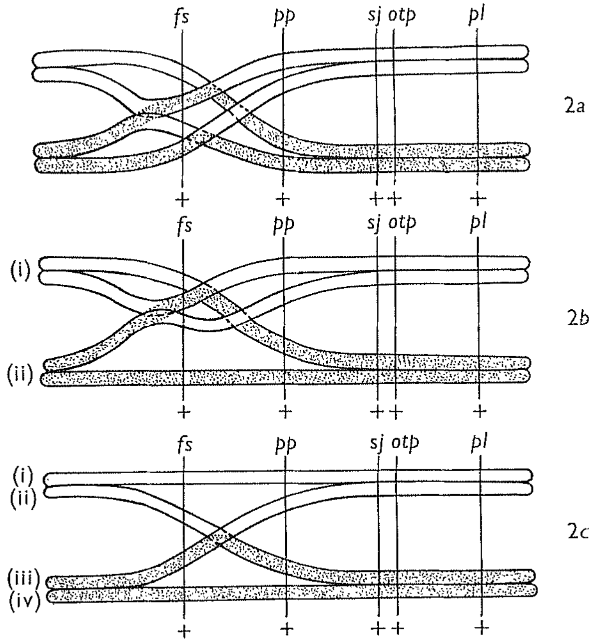

Fig. 2.

Summary

A gynandromorph in *Drosophila subobscura* segregating for autosomal mutants is described and illustrated. It can be explained as resulting from double fertilization by X- and Y-bearing sperm of reduced egg nuclei.

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