STUDIES ON THE *SAL* LOCUS IN *DROSOPHILA PSEUDOOBSCURA*.
I. THE BANDING PATTERN OF THE TIP OF SALIVARY
CHROMOSOME 3 IN LARVAE HOMOZYGOUS
AND HETEROZYGOUS FOR *SAL*¹

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ABSTRACT

In the mutant *sal* the banding pattern at the tip of chromosome 3 is changed. Certain bands are compacted instead of being partially puffed. In *sal*⁺/*sal* heterozygotes, when the chromosome tips are paired they both show the *sal*⁺ pattern or are intermediate; but when unpaired, each shows the pattern characteristic of its own genotype.

THE mutant *sal* of *Drosophila pseudoobscura* was described by LEVINE and VAN VALEN in 1962. They illustrated a difference in salivary chromosome banding pattern at the tip of chromosome 3. Further, they stated that in heterozygotes (*sal*⁺/*sal*), the paired tips of chromosome 3 both showed the *sal*⁺ banding pattern. Considering the banding pattern at the tip of 3 as a phenotypic character determined by a pair of alleles at the *sal* locus, they concluded that *sal*⁺ was completely dominant over *sal*.

I have confirmed the observations of these authors, but have also observed a phenomenon which throws doubt on the conclusion that *sal* is a recessive allele.

Photomicrographs of the tip of chromosome 3 in larvae homozygous for either *sal*⁺ or for *sal* are shown in Figure 1 A-D. Chromosome regions are numbered following TAN (1937). In both homozygotes there is a clear puff in section 80, followed distally by some heavy bands. Consistent differences between the *sal*⁺ and *sal* chromosomes are present in the terminal section 81. In *sal*⁺ (1A, B) the proximal part of this section has a number of rather indistinct wavy or dotted bands. Distal to these, the chromosome is constricted at the tip, which includes dotted and continuous bands, some of which stain heavily. In the *sal* stock (1C, D), in place of the diffuse proximal bands of section 81, there are three clear heavy bands or groups of bands (a, b, c) and the extreme tip is not constricted as compared with the rest of section 81. The marked difference in banding is due to a difference in character (density and width) of the bands at a, b, and c rather than in their number. This fact, and the difference in the diameter of the extreme tip relative to the proximal part of section 81, suggests that the *sal*⁺ chromosome is partially puffed in the region of a, b, and c as compared with the *sal* chromo-

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FIGURE 1.—Comparison of tips of chromosome 3. A, B, homozygous *sal*⁺, CH sequence; puff in section 80. C, D, homozygous *sal*, CH sequence; a, b, c, dark bands characteristic of *sal* pattern. E, F, *sal*⁺/*sal* homozygous for CH sequence. G, H, *sal*⁺/*sal* heterozygous for ST/CH sequences. G, paired tips of *sal*⁺ ST/*sal* CH. H, unpaired but approximated tips of same genotype. $\times$ ca. 2800.

some, the diffuse character of the bands in *sal*⁺ perhaps being due to a greater degree of extension of the DNA of this region than in the compacted bands of *sal*.

In Figure 1 E, F, are shown photomicrographs of *sal*⁺/*sal* heterozygotes which are homozygous for the Chiricahua (CH) gene sequence in chromosome 3 (DOBZHANSKY and STURTEVANT 1938). In such larvae the tips of chromosome 3 are paired and consistently show the banding pattern of *sal*⁺ with the puffing

of the proximal part of section 81. In larvae of the constitution sal^+ ST/ sal CH (heterozygous for sal and also for the CH inversion sequence and the standard (ST) sequence) the tips of 3 are not always paired. When paired, the bands of groups a, b and c may resemble those of homozygous sal^+ larvae, or may be heavier than usual, having an appearance somewhat intermediate between sal^+ and sal (Figure 1G). When unpaired, one tip is clearly of the sal^+ and the other of the sal banding type (Figure 1H). The former can be identified as belonging to the chromosome with the ST sequence and the latter as having the CH sequence. Thus the banding pattern of each chromosome is autonomous when they are unpaired, even though the pattern of the sal chromosome is modified when it is synapsed with a sal^+ homologue.

Similar behavior of a puffed region has been discussed by ASHBURNER (1967). In larvae of which only one parent is characterized by a specific puff, this puff may be manifested in only one of the paired homologues (BEERMANN 1952; HSU and LIU 1948; PANITZ 1965) or in both (ASHBURNER 1967; MECHELKE 1960). The questions raised by the present example are whether it is valid to consider that sal is recessive to sal^+ or to consider the banding pattern as a phenotypic character. First, if the banding pattern is considered as a phenotypic character, insofar as it is determined independently in each chromosome (when the chromosomes are unpaired) according to the allele of sal present in that chromosome, the sal^+ allele cannot be considered dominant and the sal allele recessive in the ordinary sense. Second, if the difference in banding pattern is a function of puffing involving several bands, it is not the final phenotypic effect of an allele at the sal locus. Rather, it is itself a difference in the activity of a gene (or genes) whose end results are unknown. As long as the phenotypic character(s) determined are uncertain, it is impossible to discuss the dominance relations of the gene(s) concerned.

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LITERATURE CITED

- ASHBURNER, M., 1967 Gene activity dependent on chromosome synapsis in the polytene chromosomes of *Drosophila melanogaster*. *Nature* **214**: 1159-1160.
- BEERMANN, W., 1952 Chromomerenkonstanz und spezifische Modifikationen der Chromosomenstruktur in der Entwicklung und Organdifferenzierung von *Chironomus tentans*. *Chromosoma* **5**: 139-198.
- DOBZHANSKY, TH. and A. H. STURTEVANT, 1938 Inversions in the chromosomes of *Drosophila pseudoobscura*. *Genetics* **23**: 28-64.
- HSU, T. C. and T. T. LIU, 1948 Microgeographic analysis of a chromosomal variation in a Chinese species of *Chironomus* (Diptera). *Evolution* **2**: 49-57.
- LEVINE, L. and L. VAN VALEN, 1962 A gene in *Drosophila* that produces a new chromosomal banding pattern. *Science* **137**: 993-994.
- MECHELKE, F., 1960 Strukturmodifikationen der Speicheldrüsenchromosomen von *Acrictotopus* als Manifestation eines Positionseffektes. *Naturwiss.* **47**: 334-335.
- PANITZ, R., 1965 Heterozygote Funktionstrukturen in der Riesenchromosomen von *Acrictotopus lucidus*. Puffs als Orte unilokaler Strukturmutationen. *Chromosoma* **17**: 199-218.
- TAN, C. C., 1937 The cytological maps of the autosomes in *Drosophila pseudoobscura*. *Z. Zellforsch.* **26**: 439-461.