

occurred between antiserum and stabilized extracts of mosaic-infected apple leaf tissue in gel-diffusion tests.

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² Yarwood, C. E., *Hilgardia*, **23**, 613 (1955).

³ Tomlison, J. A., *et al.*, *Phytopath.*, **49**, 293 (1959).

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GENETICS

Distance and Sequence of the Loci for Protan and Deutan Defects and for Glucose-6-Phosphate Dehydrogenase Deficiency

PROOF for the separate localization on the human X-chromosome of the protanopia-protanomaly alleles and of the deuteranopia-deuteranomaly alleles requires the demonstration of: (1) non-allelic compound hemizygous males which in conditions of equilibrium should occur once among a thousand men (one in eighty colour-blind men) or of (2) cross-over males in families combining both classes of defect.

Reviving the one-locus theory, Stern¹ asserts that protan-deutan men have not been found or are at least exceptional. However, assessment of the existence and frequency of the various compound hemizygotes depends on the kind of colour vision expected of them; some could be *sui generis*, others difficult to distinguish from deutans, protans or normals. Walls and Mathews² consider two brothers each combining protanopic and deuteranopic features as slightly different compounds, though Stern prefers to consider them as bearers of a new allele at a single locus. Men combining features of 'red' and 'green' blindness have also been described in the older literature (see Bell³) and more recently by Jaeger⁴; they are indeed familiar to careful investigators. On the other hand, some such compounds are placed among the pure protans or deutans by insufficient testing, while others may have a sufficiently balanced colour vision to pass an anomaloscope test or may be sufficiently different from the ordinary run of colour-blind people not to fail on pseudoisochromatic charts. These uncertainties make one hesitate to deny the existence of protan-deutan hemizygotes and to dismiss the two loci hypothesis.

This hypothesis has recently been considerably strengthened by the publication of a pedigree by Vanderdonck and Verriest⁵ containing two or possibly three cross-overs between the deuteranopia and the protanomaly genes. The family consists of the offspring from a protanomalous wife (daughter of a deuteranopic man and a normal woman) and a normal husband (son of a normal man and a woman of unknown colour vision). This union produced two deuteranopic, one protanomalous and two normal sons as well as one protanomalous and one normal daughter. The colour vision of the members of this family has been expertly investigated and their nuclear sex shown to agree with apparent sex. The authors consider the two normal sons as recombinants from the X-chromosomes of their mother, one of which carries and shows a protanomaly gene and the other a deuteranopia gene. The normal daughter is not discussed.

Before attempting an estimate of the recombination fraction between the protan and deutan genes one may ask why in spite of prolonged attempts⁶ recombination has not been previously found. Women, heterozygous for protan and deutan genes, are rare (about 1 in 250), and having either near normal⁷ or atypical colour vision^{2,4} they can only be discovered through having a protan and a deutan son. At least a third son is needed to show recombination, but his chance to do so is less than a half. Fewer than a handful of such families had been previously described⁸, and as no recombinants had been found, it was concluded that the two colour vision loci are likely to be closely linked⁹. This conclusion is no longer warranted.

The distance between protan and deutan genes may also be inferred from linkage studies including other sex-linked genes. An estimate by Haldane and Smith¹⁰ of a recombination frequency of 9.8 per cent between 'colour blindness' and haemophilia, which then was not clinically subdivided, seems to be based on 16 pedigrees of deutans and only one small pedigree of protans. Pedigrees combining colour blindness with muscular dystrophy are as yet not numerous. Porter, Schulze and McKusick¹¹ recently estimated the recombination fraction between the genes for glucose-6-phosphate dehydrogenase deficiency and that for deutan defects as 0.05 (between 0.009 and 0.18 at 90 per cent confidence-level) and the 90 per cent probability of recombination between the glucose-6-phosphate dehydrogenase gene and a protan gene as less than 0.2, and they considered their results insufficient to decide between the two loci and one locus hypotheses. However, considering Vanderdonck and Verriest's pedigree it is at present reasonable to assume that the protan locus and the deutan locus are not very close and that perhaps the locus for glucose-6-phosphate dehydrogenase deficiency lies between them, probably nearer to the deutan locus.

The position of these three loci should be considered in the linkage studies with the sex-linked blood group antigen, promised by Mann *et al.*¹².

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An Unusual Bi-paternal Litter in Sheep from a Natural Double Mating

ALTHOUGH it is known that many cases of naturally occurring bi-paternal litters are probably born each year in domestic sheep flocks no well-authenticated examples seem to have been reported. Certainly none seems to have been studied in any detail when they