NOTE ON THE INHERITANCE OF CHARACTERS IN WHICH DOMINANCE APPEARS TO BE INFLUENCED BY SEX.

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A NUMBER of cases have been described, in which it appears that a character is dominant in one sex, recessive in the other. Such cases fall into two categories, according to whether the character concerned is inherited in the normal Mendelian manner, or is sex-limited in its inheritance. Examples of the former type are the horned character in sheep (horns dominant in the male¹), and probably the white colour in the butterfly *Colias* (white dominant in the female²); of the sex-limited type examples are colour-blindness, hereditary nystagmus and haemophilia in man, and probably the orange colour in cats³. In the latter class it has frequently been stated that the character concerned is dominant in the male, recessive in the female. Taking colour-blindness as an example, we find the following facts. A colour-blind man married to a normal woman has usually only normal offspring; his sons do not transmit the affection, but his daughters transmit it to some of their male children, as in the following scheme:

A colour-blind man married to the normal daughter of a colour-blind man may have colour-blind daughters as well as sons, thus:

¹ Wood, *Journ. Agric. Science*, III. 1909, p. 145.

² Gerould, *Amer. Naturalist*, 45. 1911, p. 257. In this case there is the complication that homozygous white females have not been observed.

³ Doncaster, *Proc. Camb. Phil. Soc.* XLII. 1905, p. 35. Since the publication of that paper I have obtained evidence, not yet conclusive, that the inheritance of the orange colour is sex-limited. Experiments to test this more fully are being made.

The explanation commonly given of these facts has been that colour-blindness is dominant in the male, recessive in the female, so that the male heterozygote is colour-blind, the female heterozygote normal; a colour-blind woman can thus arise only when the affection is inherited from both parents. It is also evident that the affected male transmits the factor for the disease only to his daughters; the heterozygous female, however, transmits to some of the offspring of both sexes. This sex-limitation of the transmission makes a different explanation possible, which is also more in accord with other cases of sex-limited inheritance.

Since the male transmits the factor for colour-blindness only to his daughters, it must be assumed that the male in this case is heterozygous for the sex-determiner. In former papers I have suggested that if maleness is determined by a factor ♂, femaleness by a factor ♀ epistatic to ♂ when both are present, then a male individual may be represented ♂*O*, a female ♂♀; i.e. that both sexes are heterozygous for sex-determiners, with selective fertilisation between ♂-bearing eggs and *O*-bearing spermatozoa, and between ♀-bearing eggs and ♂-bearing spermatozoa¹. If we adopt this scheme as a working hypothesis, and then represent normal sight by *N*, colour-blindness by absence or modification of *N* (= *n*), and further suppose that *N* can only be borne by gametes containing a sex-determiner (♂ or ♀, not *O*), we obtain the observed results.

Parents	$n\sigma O$ (affected male)	×	$N\sigma N\varphi$ (normal female)
gametes	$n\sigma, O$	⋮	$N\sigma, N\varphi$
F_1	$N\sigma O$ (normal male)	×	$n\sigma N\varphi$ (normal female heterozygous)
gametes	$N\sigma, O$	⋮	$n\sigma, N\varphi$ $N\sigma, n\varphi$
F_2	$n\sigma O$ (affected male)		$N\sigma n\varphi$ (normal female heterozygous)
	⋮		⋮
	$n\sigma O$ (affected male)	×	$N\sigma n\varphi$ (heterozygous female)
gametes	$n\sigma, O$	⋮	$N\sigma, n\varphi$ $n\sigma, N\varphi$
	$n\sigma O$ (affected male)		$n\sigma N\varphi$ (normal female heterozygous)
	$N\sigma O$ (normal male)		
			$n\sigma n\varphi$ (affected female)
			$n\sigma N\varphi$ (normal female heterozygous)

¹ *Proc. Roy. Soc. B.* 82. 1910, p. 88, B. 83. 1911, p. 476. My reasons for continuing to prefer this scheme to that of the American writers, who represent the male as *XO*, the female *XX*, will be given in a subsequent paper on the same subject. The argument in the present case applies equally to both schemes.

This scheme is exactly comparable with T. H. Morgan's results on the inheritance of the white eye in *Drosophila*¹, in which no suggestion of alternative dominance has ever been made; if N represents the factor for red eye and n its absence (white eye), the scheme does as well for *Drosophila* as for human colour-blindness.

The scheme here outlined will apply to all cases of a character apparently dominant in one sex only and also sex-limited in its transmission by that sex (with the possible exception of the orange colour in cats, the inheritance of which is not adequately known). It will not apply to cases which show no sex-limitation in inheritance (e.g. horns of sheep); in these it must probably be supposed that a sex-limited modifying factor is present in one sex.

¹ Morgan, *Science*, 32. 1910, p. 120; *American Naturalist*, 45. 1911, p. 65.