HORNS IN SHEEP AS A TYPICAL SEX-LIMITED CHARACTER

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[*Reprinted from* SCIENCE, *N. S., Vol. XXXV., No. 897, Pages 375–377, March 8, 1912*]

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SEVERAL years ago Wood (1905) published a note in which he showed that, in a cross between a Dorset Horn and a Suffolk (belonging to a hornless breed of sheep), the male offspring all developed horns but the female offspring remained hornless. He showed further that in the F_2 generation hornless males arise, and these do not carry the determiner for horns, and horned females, but only when they have the determiner duplex. Bateson (1909, p. 173) has discussed these facts and drawn the conclusion: "Sex itself acts as a specific interference, stopping or inhibiting the effects of a dominant factor, and it is not a little remarkable that the inhibition occurs always, so far as we know, in the female, never in the male." He admits, however, the difficulty in distinguishing between this probability and the other possibility; viz., that the male provides a stimulating factor. Castle (1911, p. 102) concludes that the reason horns are more strongly developed in males than females is "the presence of the male sex-gland in the body, or rather probably some substance given off into the blood from the sex gland, favoring growth of the horns"; and he adds that if the male Merino sheep (in which, usually, the male, and the male only is horned) is castrated early in life no horns are formed. He gives no reference for the last statement; and in view of the variability of the horned condition in the males of the "Merinos" the conditions of the experiments would have to be carefully considered before such a result could be accepted as settling the question of the dependence of horns in heterozygous males upon a secretion from the testis.

The hypothesis that we have adopted and which works with entire satisfaction assumes, first, that, as in man so in sheep, the male is heterozygous (simplex) in sex. One sex-chromosome is then to be expected in the male, and substantially this condition has been found to hold for man by Guyer (1910). The female will then be duplex in respect to sex. One further assumption is necessary; there is an inhibitor to horn formation, and this is located on the sex chromosome; consequently it is simplex in the male and duplex in the female. Thus it belongs to the well-known class of sex-limited characters. The inhibi-

[1] Joint contribution from the New Hampshire Agricultural Experiment Station and the Station for Experimental Evolution, Carnegie Institution of Washington.

Determiners in Germ Plasm of			No. of Horned and Hornless Offspring			
	Male	Female	Males		Females.	
			Horned	Hornless	Horned	Hornless
Soma	*XxhhIi* (hornless)	*XXhhII* (hornless)				
Gametes	*XhI*	*XhI*				
	xhi					
Zygotes	*XxhhIi* (hornless)	*XXhhII* (hornless)	0	4	0	12
Soma	*XxhhIi* (hornless)	*XXHhII* (hornless, simplex)				
Gametes	*XhI*	*XHI*				
	xhi	*XhI*				
Zygotes	*XxHhIi* (horned)	*XXHhII* (hornless)	(2)	(2)	(0)	(2)
	XxhhIi (hornless)	*XXhhII* (hornless)	2	2	0	2
Soma	*XxhhIi* (hornless)	*XXHHII* (horned)				
Gametes	*XhI*	*XHI*				
	xhi					
Zygotes	*XxHhIi* (horned)	*XXHhII* (hornless)	15	0	0	24
Soma	*XxHhIi* (horned, simplex)	*XXhhII* (hornless)				
Gametes	*XHI*	*XhI*				
	XhI					
	xHi					
	xhi					
Zygotes	*XxHhIi* (horned)	*XXHhII* (hornless)	(.5)	(.5)	(0)	(8)
	XxhhIi (hornless)	*XXhhII* (hornless)	0	1	0	8
Soma	*XxHhIi* (horned, simplex)	*XXHhII* (hornless, simplex)				
Gametes	*XHI*	*XHI*				
	XhI	*XhI*				
	xHi					
	xhi					
Zygotes	*XxHHIi* } (horned)	*XXHHII* (horned)				
	XxHhIi } (horned)	*XXHhII* } (hornless)	(7.5)	(2.5)	(2)	(6)
	XxHhIi } (horned)	*XXHhII* } (hornless)				
	XxhhIi (hornless)	*XXhhII* } (hornless)	6	4	1	7
Soma	*XxHhIi* (horned, simplex)	*XXHHII* (horned)				
Gametes	*XHI*	*XHI*				
	XhI					
	xHi					
	xhi					
Zygotes	*XxHHIi* (horned)	*XXHHII* (horned)	(10)	(0)	(4)	(4)
	XxHhIi (horned)	*XXHhII* (hornless)	10	0	4	4
Soma	*XxHHIi* (horned)	*XXhhII* (hornless)				
Gametes	*XHI*	*XhI*				
	Hhi					
Zygotes	*XxHhIi* (horned)	*XXHhII* (hornless)	5	0	0	8
Soma	*XxHHIi* (horned)	*XXHHII* (horned)				
Gametes	*XHI*	*XHI*				
	xHi					
Zygotes	*XxHHIi* (horned)	*XXHHII* (horned)	6	0	14	0

tor, then (designated in the table by the letter *I*, its absence by *i*), will always be double in the female and single in the male and, in the gametes, will always be associated with the sex-chromosome, which is designated throughout by the symbol *X*; its absence by *x*. In the zygote the single inhibitor is incapable of preventing the development of the determiner for the horn (*H*) even when the latter is only simplex. But the double inhibitor is capable of preventing the single horn (*Hh*) determiner, but not the double determiner (*HH*).

The table gives a summary of matings used, their hypothetical somatic and gametic composition, and the proportion of each sort of zygote that will be formed in each sex. The actual frequency of offspring derived from each mating is given on the left of the

table; the expected proportions in the more complex cases being given above the actual findings in parenthesis. The matings were made and the offspring examined in major part at the New Hampshire Agricultural Experiment Station and in minor part at the Station for Experimental Evolution. The latter station was able to contribute especially to the results of later generations. For horned females, Dorsets were used; for horned males Rambouillets, Dorsets and the Scottish 4-horned race. As hornless races the Downs were chiefly employed. It is not our purpose now to give complete details, as the experiments are being continued and full data will be deferred until the publication of our final report.

The results of the table accord very closely with expectation, so that we are justified in concluding that an explanation of the results like that we offer is the correct one. By our formula, then, the case of inheritance of horns in sheep is brought quite into line with that of other sex-limited characters, its peculiarities being due to an inhibitor of horn development that is carried in the sex-chromosome.

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January 29, 1912