

*A SIMPLIFIED EXPLANATION OF BELLAMY'S¹ EXPERIMENTS
CONCERNING SEX DETERMINATION IN TROPICAL FISHES*

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Individual animals are distinguished as male or female according as they produce sperm or eggs at reproduction. If an individual produces both eggs and sperm, it is known as a hermaphrodite. Production of eggs and production of sperm take place at different levels of metabolic activity, egg production involving greater development of reserve food materials for the nourishment of the future embryo, whereas the sperm includes scarcely more than the essential nuclear constituents of a gamete.

In the early years of the present century it was definitely established that the determination of the sex of individual offspring is a genetic phenomenon, involving the production by one parent, either of two kinds of eggs (potentially male and female, respectively), or of two kinds of sperm (male determining and female determining).

The first case experimentally demonstrated was that of the squash bug, *Anasa tristis*, in which two kinds of sperm are produced by the male parent (male determining and female determining, respectively), the female parent producing only a single type of egg, which after maturation contains 11 chromosomes. The sperm cells of this species differ in chromosome number, male-determining sperm containing 10 chromosomes, female-determining sperm containing 11 chromosomes. The egg which is fertilized by an 11-chromosome sperm becomes a female (with $11 + 11$ chromosomes in the zygote); the egg which is fertilized by a 10-chromosome sperm becomes a male (with $11 + 10$ chromosomes in the zygote). In this case we may speak of the male as the heterogametic sex (since it produces two unlike types of gametes) the female being homogametic (producing only one type). The odd chromosome of the male (the one without a mate) had been called the *X*-chromosome by cytologists. It now became recognized as a sex-determinant. The formula of the sexes accordingly was $XX =$ female, $XO =$ male. Later Morgan showed that in *Drosophila* the *X*-chromosome is the vehicle of sex-linked inheritance. He supposed that in the male *Drosophila* (as in the squash bug) the sex-chromosome would have no synaptic mate. But subsequent cytological study showed that it had a mate, which was designated as *Y*, but this apparently carried no genes. I pointed out the fact that if it did come to carry genes, these would be capable of transmission directly from father to son, unlike genes borne in an *X*-chromosome. This form of transmission of characters was some years later shown to exist in fishes by Schmidt and independently by Aide.

Also it was found that the *Y*-chromosome of *Drosophila* in reality may carry genes, contrary to what had previously been supposed.

The type of sex determination found in the squash bug and *Drosophila* occurs also in man and mammals generally, but in birds among the vertebrates and in moths among insects, a fundamentally different type of sex determination occurs. Here the female is the heterogametic sex and sex-linked characters are borne in a chromosome having male determining influence, which came to be called *Z*, its synaptic mate with female determining influence being called *W*. The formula of the sexes is then $ZW = \text{female}$, $ZZ = \text{male}$.

I have always regarded the difference in terminology used in describing the two types of sex determination as unfortunate and apt to be misleading and so suggested some years ago that it would simplify matters if we retained the original (*X-Y*) terminology in both cases calling a chromosome which has a female influence in sex determination always *X*, and one which has a male influence always *Y*. The constitution of the sexes would then be:

	Female	Male
In <i>Drosophila</i> and man	<i>XX</i>	<i>XY</i>
In birds and moths	<i>XY</i>	<i>YY</i>

The essential difference between the two systems would seem to consist in a difference in the relative potency of *X* and *Y*, *Y* being dominant in the *Drosophila* system and *X* in the poultry system. How such a change could have come about, we can only speculate. We find experimental evidence in the work of Bellamy that the *Drosophila* system is the original one and the poultry system the derived one. This work of Bellamy and others on sex determination and sex linked inheritance in tropical fishes is illuminating because here related species capable of being crossed have contrary types of sex determination. Bellamy has made reciprocal crosses between two species of *Platyocilus*, *P. variatus* which has the *Drosophila* type of sex determination, and *P. maculatus* which has the poultry type.

Employing the simplified terminology which I am suggesting, these crosses may be expressed thus:

	Maculatus ♂	×	Variatus ♀
Cross 1.	$Y_p Y_p$		<i>XX</i>

The maculatus *Y* chromosome bears in this cross a dominant sex-linked color gene (*pulchra*, *p*). Since both parents are homogametic, the offspring (118 in number) are all alike $X Y_p$ in formula, all *pulchra* in color and male as to sex. This result indicates that when the two types of sex-deter-

mination come into conflict, *Y* (the male influence) is dominant over *X* (the female influence) as in *Drosophila*, suggesting that to be the more primitive type.

The reciprocal cross may be expressed thus:

Variatus ♂ × Maculatus ♀

Cross 2. *XY_{st}* *XY₊*

Both parents are in this cross heterogametic, *Y* being dominant in the Variatus (male) parent and carrying a gene for striping (*st*), *X* being dominant in Maculatus, the female parent. The Maculatus parent used in this cross carried wild color (+), not *pulchra* in its *Y* chromosome. Four sorts of combination are possible, as follows:

	Variatus gametes		<i>X</i>	<i>Y_{st}</i>
	Maculatus gametes		<i>Y₊</i>	<i>X</i>
Zygotes	<i>XY₊</i>	<i>Y₊Y_{st}</i>	<i>XX</i>	<i>XY_{st}</i>
	13 ♂♂	10 ♂♂	2 ♀	1 intersex
	wild type	striped		?

The striping of 10 males indicated that they were *Y₊Y_{st}*, the non-striping of 13 other males indicated that they were *XY₊* (weak *Y* being dominant over weak *X*), as in the reciprocal cross. Two females would seem to answer to the category *XX*. One of these females mated to a brother produced an intersex, which was probably *XY* in formula.

Hybrid *F₁* males produced by Cross 1 (*XY_p* in formula) were backcrossed with females of both parent species with results which can be expressed thus:

Backcross 1. *F₁♂* × Maculatus ♀

XY_p *XY₊*

	<i>F₁</i> gametes		<i>X</i>	<i>Y_p</i>
	Maculatus gametes		<i>X</i>	<i>Y₊</i>
Zygotes	<i>XX</i>	<i>XY_p</i>	<i>XY₊</i>	<i>Y_pY₊</i>
	10 ♀♀ wild,	49 ♀♀ pulchra,	9 ♂♂ wild,	33 ♂♂ pulchra

Backcross 2. *F₁♂* × Variatus ♀

XY_p *XX*

	<i>F₁</i> gametes		<i>X</i>	<i>Y_p</i>
	Variatus gametes all		<i>X</i>	
Zygotes	<i>XX</i>		<i>XY_p</i>	
	69 ♀♀ wild type		49 ♂♂ pulchra	

Although Bellamy does not use the simplified terminology which I am suggesting, his interpretation is substantially the same as I have given. The essential points are that in *P. maculatus* sex-linked characters are borne in a *Y* (male determining chromosome) whereas in *P. variatus* they are borne in an *X* (female determining chromosome). When the two systems are brought into competition, *Y* is dominant over *X* as in *Drosophila*, this being thus indicated as the more primitive system. It is not clear what is the result when the strong *X* of one system is combined with the strong *Y* of the other system; possibly it results in the production of an intersex.

¹ Bellamy, A. W., *Proc. Nat. Acad. Sci.*, **22**, 531-536 (1936).

THE KINETIC BASIS OF CRYSTAL POLYMORPHISM

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1. *Introduction.*—The existence of a substance in several crystalline modifications and the inversions of these from one form to another are phenomena usually thought of from a very generalized thermodynamic viewpoint. Tenable specific reasons why a substance should exist in more than one modification and why these should transform to one another under various changes of conditions do not appear to have been offered. In the present paper, an attempt will be made to give such reasons by suggesting a certain dynamic-structural viewpoint. For simplicity, change of phase with pressure will be neglected and attention will be focused on the change of phase with temperature.

The necessity for some degree of periodic and symmetrical arrangement in crystals requires that there be discernible within them some sorts of coordination groups of atoms. These coordination groups are well known,¹ and Pauling has formulated rules² for the prediction of structures of ionic crystals based upon coordination. The rules do not, however, give a unique solution of the crystal structure for any given compound, for there are ordinarily a number of alternative ways of linking groups together, each of which leads to a different structure. Such alternatives are, of course, possible polymorphous modifications of the same compound. It is believed that a development of the theory presented in this paper may afford a key to the correct selection of the appropriate crystal structure from the possible alternatives.