filled with sand and rubble of corals, shells and foraminifera. The same structure is revealed in cores from borings, such as those made at Funafuti. It is the biotic cementation by the nullipore which sets off the coral reef (or island) of Darwin and his successors from other calcareous reefs, and it is the nullipore, therefore, which controls and shapes the reef from its origin to its final form. Since cementing and even what may properly be called reef-forming nullipores may be the exclusive constituents of a so-called "coral reef," and since they are, as a group of organisms, exempt from the depth limitation of "reef-forming corals," the only observation of Darwin's hypothesis (hardly a true theory) is eliminated; and his assumption of interconvertibility and the consequent assumption of subsidence during reef development are unnecessary.

THE QUANTITATIVE THEORY OF SEX AND THE GENETIC CHARACTER OF HAPLOID MALES

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Introduction.—The foundations were laid for a quantitative theory of sex by the brilliant pioneer work of Goldschmidt and Bridges.

1. Goldschmidt was led to formulate a quantitative theory of sex by his studies of the genetics of the gipsy moth. He found that when different geographical races were crossed, as for example European and Japanese, individuals of mixed sexual character were often produced which he termed intersexes. Sometimes these individuals were predominantly female, sometimes predominantly male; sometimes their change from the expected sex character was so complete as to amount to sex reversal and only unisexual broods were obtained, exclusively male or exclusively female.

Oftentimes reciprocal crosses gave unlike results, one cross producing a normal result with equal numbers of males and females, whereas the reciprocal cross would produce only females and male intersexes, or only males and female intersexes. In extreme cases the intersexes would be transformed into the opposite sex, so that unisexual broods resulted.

Goldschmidt explained these results by assuming that maleness and femaleness are determined by genes borne in different chromosomes and that the strength or potency of these genes varies from race to race. Crosses bring together male and female genes of different relative potency and this upsets the usual sex balance and produces intersexes.

2. Bridges and his co-workers reached conclusions somewhat similar
from their studies of triploid individuals of Drosophila and of their descendants. Triploids inevitably produce unbalanced chromosome conditions in a considerable proportion of their descendants, and it was from a study of these that Bridges was able to make a more complete and certain analysis of the influence on sex of each set of chromosomes than had been attempted by Goldschmidt.

The method of sex determination is also different in Drosophila from the method found in the gipsy moth (Lymantria), the form studied by Goldschmidt, and this led to minor differences in their conclusions.

Bridges found that the X-chromosome of Drosophila has a female influence which is superior to the male influence of the autosomes (II, III, and IV). Accordingly any multiple of XA (letting A stand for a complete set of autosomes) will be female. Thus 2X2A is an ordinary diploid female, 3X3A is a triploid female and 4X4A is a tetraploid female, all of which have been experimentally produced and identified. A few individuals have also been produced which were haploid (XA) in certain mosaic segments of the body which was elsewhere diploid. These haploid segments appear to be female also, as they produce no sex-combs, a male character.

But in Drosophila the female influence of X is less than the male influence of two sets of autosomes, since an individual X2A or XY2A in constitution is a male. But a 2X3A individual is an intersex in which male and female characters both find expression. Hence 2X = 3A, and X = 1.5A would be a quantitative statement of the relative potency of the respectively female and male influences of X and A.

No individual genes influencing sex have been found by students of Drosophila in any of the chromosomes, though search has been made for them, and the failure to find them is significant in view of the very complete linkage studies made on this species.

In the quantitative theory of sex as formulated by Goldschmidt and adopted by Winge and Hartmann, it is assumed that there are specific and separate genes for maleness and femaleness and that the relative strength or valence of these determines what the sex shall be in a particular organism.

But the existence of such genes has never been conclusively demonstrated, as should be possible by linkage studies if they really existed, as postulated, in particular chromosomes. Their status is purely hypothetical and, I think, superfluous.

I propose a simplified quantitative theory of sex, in accordance with which it is unnecessary to suppose that there are specific genes for maleness and femaleness, but sex differences are merely plus and minus variations in a single scale of gradations in sexual character.

_Haploid Sex Determination._—Sex is exemplified in its simplest form in a
tendency of two cells to unite to form a new individual. The uniting cells must differ from each other physiologically even when they are morphologically alike. The primary difference is perhaps in character of metabolism, as suggested many years ago by Geddes and Thompson. A more vigorously growing type, predominantly anabolic in its metabolism, can be distinguished from a less vigorously vegetative type predominantly katabolic in its metabolism. Blakeslee (1904) when he discovered the existence of sexual differentiation among bread-moulds and related fungi distinguished one type as +, the other as −. He found that sexual union could occur only between a+ and a− strain. Among the algae a similar differentiation exists, as shown by Schreiber (1925) in the case of Gonium. The swarm spores (gametes) which unite in pairs are all motile and morphologically alike but fall into two classes + and − in sexual reaction.

\[ \begin{array}{cccc}
\text{Strong} & \text{Weak} & \text{Weak} & \text{Strong} \\
\varphi & \varphi & \sigma' & \sigma' \\
+ & + & - & - \\
\end{array} \]

**FIGURE 1**

Hypothetical sex gradient.

Unions occur only between a + and a − gamete, and these arise from different haploid clones. The diploid zygospore on germinating produces four haploid cells by a reduction division followed by an equational division. Two of these cells are plus, two are minus in sex character. Each transmits in its gametes its own sex tendency.

The essential primary feature of sexuality appears to be differentiation of gametes in opposite directions (+ and −) along a gradient of some sort. See figure 1. Ordinarily sexual union occurs only between gametes which are differentiated in opposite directions from a zero or indifferent state, so that one is *plus*, the other *minus*. But exceptionally, as pointed out by Hartmann, union may occur between two minus or two plus gametes, if they are sufficiently different in the strength of their sex tendency. Thus
in Ectocarpus, a strong minus may occasionally unite with a weak minus; and in Dasycladus, according to Jollos (1926), a strong plus may unite with a weak plus, as well as a strong minus with a weak minus.

The regular thing is for any plus to unite with any minus, but exceptionally plus will unite with plus or minus with minus, if the two are far apart in strength of sex tendency.

This is the phenomenon which Hartmann calls relative sexuality, in accordance with which a cell which is ordinarily male in its reaction will function as a female in relation to other male gametes, if they are strongly

male and it is weakly male (that is, close to the zero or dividing line between maleness and femaleness).

Diploid Sex Determination.—As we pass upward in the organic scale, we find that plus and minus gametes become morphologically different. The former become non-motile and accumulate reserves of nourishment and are known as eggs; the latter retain a high degree of motility, do not store nourishment except for immediate use and are known as sperms. Sexual union can now occur only between egg and sperm.

In the higher animals and plants, the diploid or zygote stage becomes

![Diagram of sex determination in Drosophila and mammals](image-url)
increasingly important and occupies a more prominent place in the life cycle. And individuals become differentiated according to the kind of gamete which they produce, eggs or sperm. Those which produce eggs only, we call females; those which produce sperm only, we call males. We should naturally expect all eggs to be + and all sperms to be - in sex tendency, but such is not the case. If it were, all zygotes would of necessity be neuter, or else all of one sex, since only one type of sexual union (+ with -) could obtain.

In order to have two types of diploid sexual individuals produced, it is necessary either (a) that part of the sperm carry the plus tendency, or (b) that part of the eggs carry the minus tendency. Both conditions obtain, the former in Drosophila and man, the latter in birds and moths. Both also occur in different species of the same group of fresh-water fishes.

The mechanism of sex determination in the sexually dimorphic animals and plants is known as an X-Y chromosome apparatus. The X-chromosome is a chromosome with a plus (or female) sex tendency, the Y-chromosome is the synaptic mate of X with a negligible (neuter) or else minus
(male) sex tendency. Two fundamentally different types of sex determination are known.

I. In Drosophila and man, and in mammals generally (Fig. 2), the sex tendency of X is weak in comparison with that of Y (and associated autosomes) so that an individual containing both is a male, XY. It takes a double dose of X (with a plus tendency) to offset the influence of Y and associated autosomes (having a minus tendency). Normal females indeed contain no Y and are XX in formula, but Bridges has shown that XXX individuals can be produced under certain circumstances and they are also female in sex (egg producers). Hence 2X > Y, the net outcome of such a combination being a female.

II. In birds and moths (Fig. 3) the plus sex tendency of X is strong in relation to the minus sex tendency of the Y chromosome (and associated autosomes). Thus an XY individual is a female because here X > Y. Males do not contain an X chromosome in birds and moths but are YY in formula. They do not produce any spermatozoa bearing a plus sex tendency, whereas in Drosophila half the spermatozoa are plus in tendency.

On the other hand, female birds and moths produce 50 per cent of eggs having a minus tendency, whereas all the eggs of Drosophila have a plus tendency.

Goldschmidt assumes (and probably correctly) that the net sex influence of the autosomes is in moths female, not male as in Drosophila, since otherwise there would be no chromosomes in the male moth having a female influence, as both (Y) sex chromosomes have a male influence. Unless such female influence is present, it would be difficult to account for the production of male (YY) intersexes, males showing female characteristics.¹

The Y-chromosome in Drosophila does not seem to have any pronounced sex tendency, though its presence is apparently essential to the production of sperm, since X2A males (lacking Y) are sterile.

In fishes, such as Lebistes, the Y-chromosome bears the genes of sex-linked characters and these may cross over to X in XY (male) individuals. In Drosophila (exceptionally among animals and plants) no crossing-over occurs in male individuals in any category of chromosomes.

In the bird and moth type of sex-determination Y seems to be a more important structure. For males contain no X at all but are homozygous for Y, which transmits sex-linked characters.

Winge has shown that in the fish, Lebistes, sex determination and sex-linked inheritance are of the Drosophila type, the male being heterozygous. It is probable that in Lebistes also the autosomes have a net sex tendency of a minus character. For Winge has been able by some undetermined chromosome combination to obtain individuals somatically male (producers of sperm) which contained two X chromosomes and so should through their influence alone have been female. None of the sperm which
they produced transmitted a *minus* sex tendency, for when they were mated with ordinary females, only female progeny were produced to the number of 314. Genetically then these males were females and they bred like females though through the medium of plus-bearing sperm, of which normal males in this species form only fifty per cent.

*The Problematical Haploid Males.*—In many animal groups (hymenoptera, scale insects, rotifers) males of a peculiar character are produced, since they arise only from unfertilized reduced eggs and so are haploid, yet they transmit in their sperm only the plus (female) sex tendency. Their spermatogenesis, too, is peculiar, since no reduction division occurs but the constitution of the egg after its reduction to the haploid state is handed on intact in its spermatozoa. A haploid male is accordingly a mechanism for the transmission of the female sex character through the agency of spermatozoa. Or better, we may regard such a haploid male as an animated $XA$ egg, which has had sufficient vitality to develop without the stimulus and nuclear reinforcement normally supplied by fertilization. Its feebler haploid state (perhaps) causes it to form sperms rather than eggs but these sperms transmit the plus sex-tendency for which the mother was homozygous.

There is, then, on this interpretation no genetic transmission of a minus sex-tendency in species which have haploid males. The egg is homozygous for plus sex-tendency ($XX$); the haploid male transmits in its one class of sperm this same sex-tendency ($X$). The $Y$ sperm of the *Drosophila* type of sex-determination has been lost from the species.

What makes these haploid individuals somatically male (producers of sperm rather than eggs), we are at present unable to state. Genetically they are female; phenotypically or somatically only are they male.

A comparative study of the scale insects shows by what phylogenetic steps haploid males have probably arisen and from which type of sex-determination they are derived.

Most species of (coccid) scale-insects produce haploid males by the same process as the honey-bee and hymenoptera generally (Hughes-Schrader). See figure 4. The egg always undergoes reduction and may develop either fertilized or unfertilized. If unfertilized, it produces a haploid male. If fertilized, it produces diploid females. The female as regards sex chromosomes is $XX$. No other hypothesis will satisfy the observed facts. The reduced haploid egg will be $X$, and the spermatozoa produced by the haploid male must also be $X$ in formula. In *Drosophila* half the spermatozoa are of this character, the other half bear $Y$. Haploid males produce *only* the $X$ (or female-determining) sperm.

Conditions in *Lecanium hesperidum*, as they are reported by Thomsen (1927), are instructive in this connection. Two races are known in this species. One of these occurs only in the female sex and reproduces ex-
clusively by diploid parthenogenesis by means of unreduced and unfertilized eggs. In the other race both sexes are known and both are diploid. Fertilized eggs may produce either sex, so the sperm are presumably dimorphic, X or Y, as in Drosophila, and all offspring so produced are either XX (female) or XY (male). But the unfertilized egg does not develop into a haploid individual (as in most scale insects). It is probably prevented from doing so by a fusion which takes place between the haploid egg nucleus and the haploid second polar-cell nucleus. Thus the diploid state is restored, but the resulting zygote is always female, never male in character, as it might have been had it been fertilized by Y sperm. This result shows that the polar-cell nucleus performs here the same function as regards sex determination as one class of sperm would have done, namely, the X sperm. And it is that class of sperm which haploid males produce exclusively in other species of scale insects.

These cases indicate clearly that it is from the Drosophila type of sex determination (the weak X type) that haploid males have been evolved. Females are XX2A in formula. At one time in all probability in these species XY2A males occurred but the Y chromosome has been lost from the
species, and sperm producers have arisen from haploid eggs which are XA in constitution. These are genetically females; functionally they are sperm producers and so are called males, but only on the basis of their somatic character.

1 Goldschmidt uses X where I use Y in describing sex determination in moths. I am avoiding that terminology so as to have X stand for plus (female) sex tendency in both schemes of sex determination.

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A CYTOLOGICAL DEMONSTRATION OF THE LOCATION OF AN INTERCHANGE BETWEEN TWO NON-HOMOLOGOUS CHROMOSOMES OF ZEA MAJS

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It has been suggested (Brink,1 Brink and Burnham2) that semisterility in maize is associated with some form of chromosomal change involving non-homologous chromosomes. Burnham3 reported the presence of a ring of four chromosomes in diakinesis in such semisterile plants which could be explained by assuming either translocation or segmental interchange. Plants showing a ring of four chromosomes in diakinesis and 50% sterility in pollen and eggs gave, when crossed with normal plants, an F1 generation, one-half of which were normal and one-half of which were 50% sterile. A semisterile plant when selfed gave, again, one-half semi-sterile plants and one-half non-sterile plants, but one-half of the non-sterile plants were homozygous for the translocation or interchange. When