CROSSING-OVER BETWEEN THE *X*- AND THE *Y*-CHROMOSOME IN *LEBISTES*.

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(With One Text-figure.)

In a paper on inheritance in *Lebistes reticulatus* (1922 *b*), discussing sex-linked as well as one-sided male inheritance, I mentioned an observation of crossing-over between the *X*- and the *Y*-chromosome in the male *Lebistes* and stated that further details would be published later. It is the object of the present report to fulfil this promise.

In the work of Schmidt on *Lebistes* (1920), the first unquestionable case was brought forward on conditions of inheritance which pointed to factors connected with the *Y*-chromosome. The investigations made by me, at a later date, on the cytological conditions in *Lebistes* (1922 *a*), have shown that the diploid chromosome number was 46 in both sexes—and in my first-named paper I stated, as the most important result of my experimental cross-breedings that, notwithstanding the lack of any visible difference between the chromosomes themselves, the male *Lebistes* decidedly belonged to the *XY*-type and the female to the *XX*-type, as is the case with *Drosophila melanogaster*. From the one-sided male inheritance, which could only be explained by assuming the existence of a factor-bearing *Y*-chromosome, one must logically conclude that *X*-chromosomes were also present and, thus, that the expression for the female chromosomes was $44 + X + X$, that of the male one $44 + X + Y$.

Moreover, I was able to prove sex-linked inheritance in at least one of the *Lebistes*-"races" which I worked on, a further instance of the indubitable conformity between the results of genetical and cytological investigations.

At the time I communicated the first case of crossing-over between the *X*- and *Y*-chromosomes,—a phenomenon which had not hitherto been brought to light for the simple reason that no factor-bearing

Y- (or *W*-) chromosome had hitherto been known with certainty to exist—I had no idea that another person was studying the same matter and had simultaneously arrived at the same results as I had.

The Japanese scientist, Aida, has undertaken extensive experimental crossings with another species of fish, the *Aplocheilus* (*Haplochilus*) *latipes*, belonging to the Poeciliidae family, published in *Genetics*, Vol. VI. 1921, p. 554[1]. In this paper, he not only proves the one-sided male inheritance, but also the crossing-over between the *X*- and the *Y*-chromosome, so that our two observations must be said to cover each other. However, no cytological investigation of the material worked on by Aida has been published as yet.

As in my own case, Aida has studied colour-factors which he found to be present in the autosomes as well as in the sex-chromosomes. In one case he discovered homozygoty for a factor *R* (red), i.e. the "race" concerned carries the *R*-factor in the *X*- as well as in the *Y*-chromosome. In cross-over individuals segregated from heterozygotic males, the conditions of inheritance are exactly as would be expected on the supposition that the factor in question (*R*) had been transferred from the *X*- to the *Y*-chromosome.

While, in *Lebistes*, the colour-factors manifest themselves in male individuals only, the inheritance being phenotypically sex-limited to the male—a fact which has not made my researches any easier—the colour-factors appear in both sexes of *Aplocheilus*. There is another slight divergency in our investigations, viz. while the *Lebistes*-factors influence patterns and various colours in certain parts of male individuals, the *Aplocheilus*-factors involve a, so to speak, total differentiation of colour in the individuals.

Hitherto, only the *R*-factor (allelomorph *r*) has been found in the *X*- and *Y*-chromosomes of *Aplocheilus*; while in *Lebistes* the *Y*-chromosome has been proved to contain a whole series of factors, and the *X*-chromosome, until now, only one factor, *s*, which has been seen only in one instance to cross over, *partially*, to the *Y*-chromosome, the said factor *s* being a complex factor composed of a series of linked factors. On the other hand, no colour-factors have, as yet, been found in the autosomes of *Lebistes*, whereas Aida has recorded the factor *B* and its allelomorphs B_1 and *b*.

In neglecting these minor differences, the results concerning the two species of fish must be said to confirm each other.

[1] This part of *Genetics* appeared Nov. 1922, though bearing date Nov. 1921.

As to the genetical formulae, Aida and myself use unlike expressions to which I shall revert below, in connection with the presence-absence theory.

I shall now proceed to the relation of my experiments on the crossing-over between *X*- and *Y*-chromosomes.

Experiments on X-Y Crossing-over.

In June 1917, while I was attached to the Carlsberg Laboratory, we received a male *Lebistes* which, in the main, had the appearance of the afore-mentioned (1922 *b*) "Spot Race" of which the males have the formula X_oY_m. The fish was bought from a Mr Christensen, Poppelgade (= Poplarstreet), Copenhagen, who, in his turn, had received it from Berlin, in the summer 1916, from a dealer in aquaria.

This new type had the following characteristics in common with "Spot Race" males, viz. (1) large black spot on dorsal fin; (2) large red side-patch below and in front of dorsal fin; (3) black dot near anal aperture; all being due to the *maculatus*-factor *m* in the male *Y*-chromosome. But whereas all the "Spot Race" males I had hitherto seen possessed a rounded, colourless caudal fin, the above male had (4) a caudal fin with elongated upper edge and (5) vivid reddish-yellow colouring on upper and lower edge of caudal fin.

This "Poplarstreet" male No. 123, as it was named after the place where it was bought, was mated, on June 9, 1917, with a virgin female No. 125 without factors in the *X*-chromosomes and, therefore, corresponding to formula X_oX_o, whereupon the female bore, until Dec. 27, 1917, six broods numbering more than 200 young ones in all. 73 young males became adult, but only one of these had the elongated caudal fin of the "Poplarstreet" male, all the others having the rounded colourless caudal fin of the "Spot Race."

Accordingly, the factor *e* (*elongatus*), responsible for the elongated caudal fin, must be supposed to reside in the male *X*-chromosome, which we know to pass on to the daughters; and we may also surmise that the single male with an elongated caudal fin owes its existence to the crossing-over, in a single case, of the *e*-factor to the *Y*-chromosome of a spermatocyte. The original "Poplarstreet" male having thus the formula X_eX_m, and therefore usually forming sexual cells carrying either X_e or X_m, it must have happened at the crossing-over that, in an isolated case, the *e*-factor was transferred to the *Y*-chromosome and then linked to the *m*-factor there. The formula of the diverging male should therefore be X_oY_{em}.

The inference, that the crossing-over between the X- and the Y-chromosome has really taken place here, is fully confirmed by the following crossing-experiments undertaken as a check. The process of analysis is represented in Fig. 1, under the form of a genealogical diagram.

As far as the non-cross-over individuals are concerned, the F_1-females of this category are supposed to have the formula $X_o X_e$ and, in mating these females with F_1-males, the formula of which is $X_o Y_m$, the outcome should be an equal number of males with elongated caudal fin, and without. In accordance with this, F_2 gave 26 $X_e Y_m$ and 27 $X_o Y_m$. The F_2-females were also expected to consist of two categories, partly $X_o X_o$, partly $X_e X_o$, and in fact, one F_2-female, mated with a "Spot Race" male ($X_o Y_m$), produced only $X_o Y_m$-males (11 in all) and therefore had the formula $X_o X_o$, while another F_2-female, mated with the same male, gave 4 males with elongated caudal fin ($X_e Y_m$) and 3 without ($X_o Y_m$); consequently, this latter F_2-female must have had the formula $X_e X_o$.

As stated above, the non-cross-over males should, theoretically, have the formula $X_o Y_m$, and their structure entirely corresponded thereto, i.e. rounded caudal fin and the general appearance of the "Spot Race." As a matter of fact, some such F_1-males, crossed with $X_o X_o$-females, produced exclusively round-tailed progeny. 22 sons in all were counted and none of these showed any trace of the e-factor.

It has thus been proved that the elongated caudal fin of the "Poplar-street" race is due to a factor in the male X-chromosome and that, therefore, the original male must have had the formula $X_e Y_m$. While the inheritance of factor m is one-sided male, the e-factor is sex-linked in its inheritance.

We shall now examine the conditions of the diverging F_1-male with the elongated caudal fin, so as to find out whether its genetical behaviour corresponds to the hypothesis that the e-factor has crossed over to the Y-chromosome, making the formula of the individual $= X_o Y_{em}$.

The male progeny of such a male should, of course, always be provided with an elongated tail-fin, all the sons receiving the Y-chromosome. Only in case of a renewed crossing-over could the e-factor again be separated from the m-factor and round-tailed sons be segregated.

All the 11 sons of the diverging male proved to have an elongated caudal fin, and this is already a proof that the e-factor has no longer its seat in the X-chromosome, but in Y and that, therefore, a crossing-over between X and Y must have taken place.

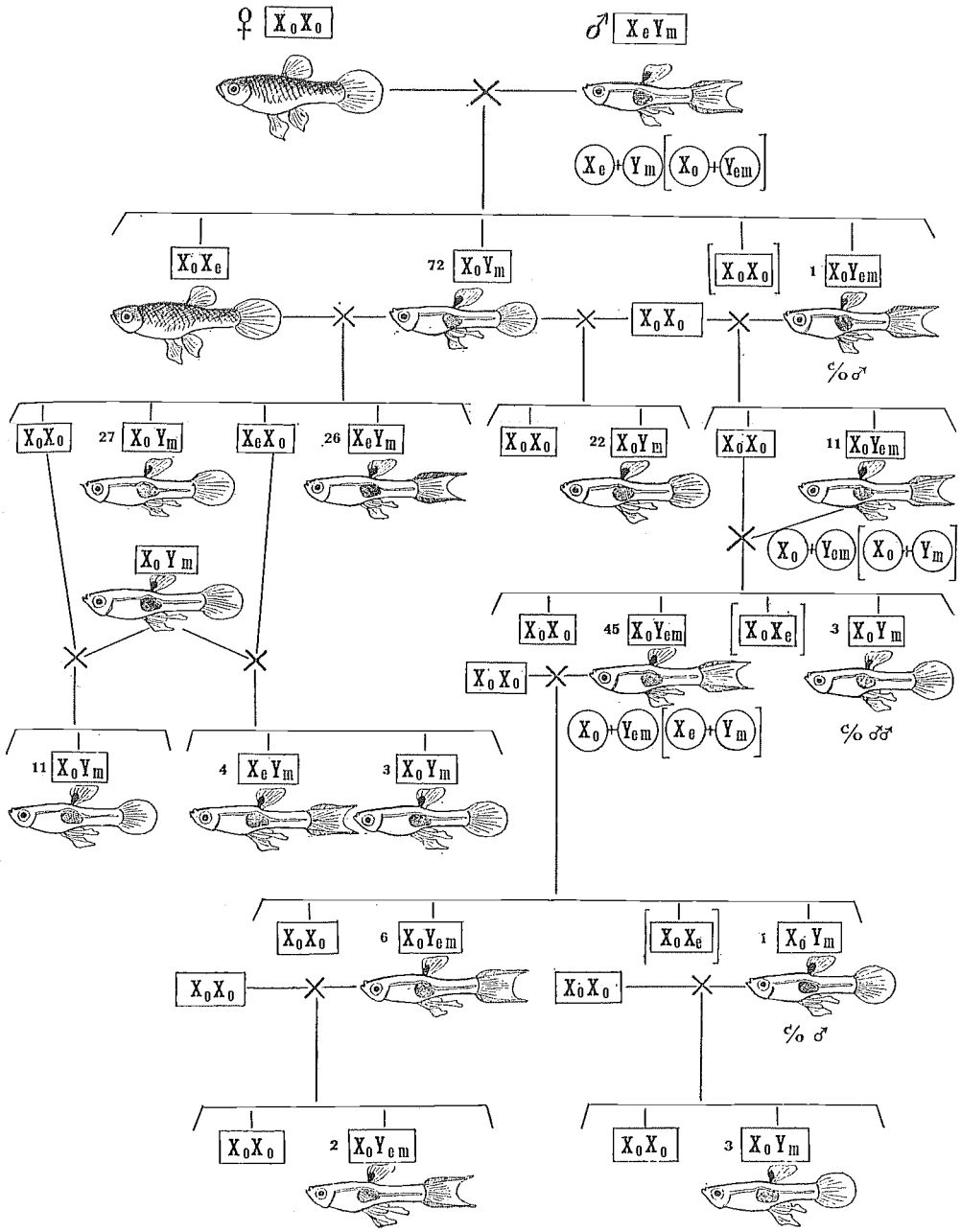
♀ XoXo
♂ XeYm
Xe + Ym [Xo + Yem]
XoXe
72 XoYm
[XoXo]
1 XoYem
♂/o ♂
XoXo
27 XoYm
XeXo
26 XeYm
XoXo
22 XoYm
XoXo
11 XoYem
Xo + Yem [Xo + Ym]
XoYm
XoXo
45 XoYem
[XoXe]
3 XoYm
Xo + Yem [Xe + Ym]
♂/o ♂♂
11 XoYm
4 XeYm
3 XoYm
XoXo
6 XoYem
[XoXe]
1 XoYm
♂/o ♂
XoXo
2 XoYem
XoXo
3 XoYm

Fig. 1.

The sequel of the analysis gave the following result: The 11 $X_o Y_m$-males were mated with some sisters which should correspond to formula $X_o X_o$, thus giving rise to a new generation, F_2, of cross-over males. As to the males, this generation consisted of 45 $X_o Y_{em}$ and 3 $X_o Y_m$. In this connection, the 45 young ones are non-cross-over individuals, whereas the 3 are the result of a new crossing-over in which the Y-chromosome has again lost its e-factor, the latter having crossed back to the X-chromosome, its original position.

Among the offspring of the 45 $X_o Y_{em}$-males, as shown in Fig. 1, was again found 1 round-tailed $X_o Y_m$-male, the result of a new crossing-over. As might be expected, this male, when mated with an $X_o X_o$-female, reproduced exclusively its own type, while the other individuals of this and the following generation all have the elongated caudal fin and the formula $X_o Y_{em}$.

Cross-over females are of course not so easily discerned as are cross-over males, as the females phenotypically show no colours at all. The only way in which we can recognize the factor-contents of a female individual is through crossing it with a male of well-known genetic constitution.

In a single case I have found such a primary cross-over female. All the female progeny from a cross-over male, $X_o Y_{em}$, with a female, $X_o X_o$, will be $X_o X_o$ if no crossing-over between X and Y in the male happens. An $X_o X_e$ female only can arise through crossing-over. Among the F_3 offspring of the primary cross-over male, $X_o Y_{em}$, with an $X_o X_o$ female, 6 female individuals were analyzed by pairing them with $X_o Y_m$ males (Spot Race). The five bore only $X_o Y_m$ males, 32 in all, and were therefore ordinary $X_o X_o$ females, but No. 6 has until now borne 2 $X_e Y_m$ males and 3 $X_o Y_m$ and must therefore have the formula $X_o X_e$, i.e. be a female individual arisen through crossing-over in an $X_o Y_{em}$ male.

We have thus proved that the e-factor, accountable for the elongated, coloured caudal fin of the original male individual, had its seat in the X-chromosome and was, therefore, sex-linked in inheritance ($X_e Y_m$). By crossing-over between the X- and the Y-chromosome, it was, in one case out of 73, transferred to the Y-chromosome ($X_o Y_{em}$), whereupon the inheritance of the elongated caudal fin became subsequently one-sided male. In the 4 male individuals out of 68, the Y-chromosome had again lost its e-factor which had anew crossed back to the X-chromosome, where it was found in a female individual.

An individual belonging, in all evidence, to the above-mentioned "Poplarstreet Race," was bought in Sept. 1917, from another Copen-

hagen dealer in aquaria and was said to have arrived from Dresden a month earlier. The race was, in all respects, similar to the "Poplarstreet Race" and, after a cross with a "Spot Race" female X_oX_o, offspring resulted, of which 22 were males, all with a rounded, colourless tail, showing that, in this individual also, the *e*-factor had its seat in the *X*-chromosome and that this male, therefore, also had the formula X_eY_m.

The whole matter will now appear clear and we shall therefore discuss the deductions which may be made.

Theoretical Considerations.

In the present and in a former report, I have shown that crossing-over between the *X*- and the *Y*-chromosome takes place in *Lebistes* and that the sole real difference between their *X*- and *Y*-chromosomes is that the *Y*-chromosome contains a dominant male factor, while the *X*-chromosome contains a recessive female factor. The *e*-factor, which produces the elongated, coloured caudal fin, may cross over from *X* to *Y* and vice versa, which, in other words, means that the male and the female factor are evidently allelomorphs which, like other factors, may be exchanged between the chromosomes. Nor has a cytological examination revealed any morphological difference between the *X*- and the *Y*-chromosomes.

Therefore, if it be true that the *Y*-chromosome contains a special male factor, this factor must be rather strongly linked to the *e*-factor, for only one cross-over individual has been found among the 73 sons of an X_eY_m-male and 4 cross-over individuals among 68 sons of X_oX_{em}-males.

It is remarkable that crossing-over has not been equally frequent in both directions; however, as the amount of material was not very large, I do not feel justified in attaching any significance to this fact. Much stronger is, however, the linkage between the male factor and other factors found in the *Y*-chromosome, such as *m* (*maculatus*), *i* (*iridescens*), etc. and the circumstance itself of diversity in the degree of linkage between sex- and colour-factors must be taken as evidence of a real gene, corresponding to the sex-factor, embodied in the chromosome and comparable with other genes. As to the *m*-factor, thousands of individuals, produced after mating of X_oX_o-females with X_oY_m-males, have been examined without one single individual with the *m*-factor missing being found. This is very striking. At the outset, one sees no reason why these factors should be located so close to the male factor that no crossing-

over can take place, but, as stated above, it is quite possible that the male factor itself is identical with the *m*-factor, although in that case one must arrive at the conclusion that, with regard to sex-factors, multiple allelomorphs exist. Another explanation of the strong linkage of these colour-factors to the sex-factor would be that crossing-over is rather rare in *Lebistes*. As said in my earlier paper (1922 *a*), I have looked in vain for a typical stage of synapsis in the spermatocytes, and neither has diakinesis been observed. Perhaps the explanation of the strong linkage might also be that only factors situated at some distance from each other can be exchanged, on account of a pronounced rigidity of the chromosomes.

It is certain that great difficulties prevent a close study of the topography of the *Y*-chromosome; for on one hand, the linkage between the colour-factors and the sex-factor appears to be strong, while, on the other hand, the factor-contents of the female individuals cannot be directly ascertained. The future must decide whether factors will be found which are linked to the sex-factors in a sufficiently variable degree to make charting of the sex-chromosomes feasible. It is obvious that, in any case, as far as *Lebistes reticulatus* is concerned, many colour-factors exist which have not yet been analysed, for, although the variations of appearance within one single race are limited, a considerable number of *Lebistes*-types are found with dealers in aquaria as well as wild.

I have mentioned that, in several of the *Lebistes*-races examined, the *X*-chromosome is empty, e.g. in the " Spot Race," and have therefore been given the sign X_o. In this case, as well as in all other *Lebistes*-races observed, the *Y*-chromosome alone contains a colour-factor. In comparing this circumstance with the fact that the *Y*-chromosome of *Drosophila* is empty, the comparison is not entirely to the point, in as far as I have reckoned with the existence of a female factor in the *X*-chromosome of *Lebistes*, whereas the existence of a corresponding male factor in the *Y*-chromosome of *Drosophila* has not been proved. On the contrary, according to the latest, very interesting researches of Bridges (1922), on flies with an abnormal set of chromosomes, it seems as though the ratio between the numbers of autosomes and of *X*-chromosomes alone determines the sex in *Drosophila*.

At any rate, factors in *Lebistes* have been found, as yet, only in the sex-chromosomes, while not one has been discovered in the 22 autosomes. Notwithstanding this, the autosomes are undoubtedly factor-bearing, even if no special colour-factor exist in them. We do not know yet in how far species determining chromatin is present in the chromo-

somes and whether it is common to all the chromosomes of one species. As only fundamental *differences* can be made the object of inheritance researches, nothing hinders the supposition that a great many species factors exist homozygotically in all the biotypes of the species, and it is even probable that several chromosome-pairs contain, in principle, the same specific factors. This latter hypothesis seems to be confirmed to some extent by the fact that numerical progressions in the number of chromosomes are found within systematic genera of the vegetable kingdom, e.g. 7, 14, 21 (*Triticum*) or 9, 18, 27, 36, 45 (*Chrysanthemum*), etc., which progressions can only be explained by supposing that the higher numbers are the result of the addition of two lower chromosome numbers after hybridization—or the doubling of the original chromosome-set. New polyploid species, originated by hybridizing two earlier species, with a simultaneous doubling of the chromosomes,—the probability of which I have established in previous researches (1917)—will have the genus-fixing factors redoubled, but this feature is not traceable in the descendency of the new types, because they are homozygotic in the genus-fixing factors, or even several times homozygotic. The fact that polymeric factors frequently occur in polyploid species—well known for instance from Nilsson-Ehle's studies of *Avena sativa* and *Triticum vulgare*—fully agrees with the supposition that the factors are repeated several times in the polyploid species; and it is quite natural to assume that even species which, on account of their number of chromosomes, do not reveal themselves as polyploid, contain many specific generic factors which are common to all the chromosomes. Some chromosome researches seem to show that adhesion between originally freely "mendelizing" chromosomes may take place; and a chronic conjugation of chromosomes, in connection with above conditions, will result in a gradual, manifold appearance of the same factors in each single chromosome—or, in any case, in more than one.

According to this, all genera of a given family should be characterized by the factors peculiar to that family, but they should be distinguished from each other by "genus-factors." All the species of a genus should contain identical factors, characteristic of that genus only, and furthermore a great many factors distinctive of the family, and be distinguished from each other only by a smaller number of specific species factors. All the varieties within one species should, homozygotically, contain identical "species-factors" beside the particular genus- and family-factors which will probably be present in several or in all the chromosomes—and they should be mutually distinguished by one or a few "variety-

factors" having their seat in one or in a few chromosomes, and disclosing themselves in Mendelian segregation when the varieties are crossed.

As two varieties, chosen within a species, only differ as far as a few factors, the "variety-factors," are concerned, but are homozygotic and isogenous with regard to all the species-, genus-, family-, etc. factors, the effect of variety-factors is alone observed in segregations. The larger the systematic unit under consideration, the more often must the genes, characteristic of that unit, be repeated in all the chromosomes.

Of course, one could not think of any absolute boundary between, for instance, "species-factors" and "variety-factors," but we must suppose that, in substance, those factors which are widely represented in all the chromosomes afford a basis for classification into large, systematic units; their frequent presence in the chromosomes will entirely prevent a segregation into types in which these factors are lacking and, with them, the corresponding morphological and physiological particularities; and the loss or the modification of a few such factors could hardly provoke any immediately visible mutation, because many others of the same nature would be left. At the most, this eventuality could be imagined to tend, throughout a long period of time, towards a slow shift in the characters of the species—a condition of things which might be associated with biological evolution.

The Presence-Absence Theory. The Denomination of Factors.

According to the opinion of many geneticists, on the nature of factors, the type holding the dominant factor contains a gene which is missing in the type holding the recessive factor. This theory has been named the "Presence-Absence Theory." It can be said to have given satisfaction until multiple allelomorphs were recorded, but after that it fell short, as the existence of a certain number of *different* types, all recessive to one and the same dominant type, could of course not be explained by the absence of the gene corresponding to the dominant factor. The notion imposed itself that, like the dominant type, the recessive type possesses a gene, but that this gene differs in value from that of the dominant type—and has a different value in the different recessive allelomorphs. According to this, multiple allelomorphs should originate from genes, diverse in value, but having the same location in the chromosomes. This conception is unquestionably gaining ground.

It has been seen from my *Lebistes*-formulae that I use the denomination X_o for an X-chromosome which contains no colour-factors, i.e. a

mode of denomination in conformity with the original conception,—and this has been done deliberately.

Aida applies the formula $R_x r_y$ to a male which I would designate by $X_r Y_o$. In the first place, Aida uses X and Y as indexes showing the location of the factors considered and thereby gives more prominence to said factors. In my own work, I have made a rule of using the factors as indexes to the chromosome-denominations, for the reason that, to keep abreast with the recording of more and more factors in each chromosome, an expression as, for instance, $AAX_{rspn}Y_{rv}$ admits, according to my idea, of more rapid discrimination than $AAR_xR_yS_xP_xN_xV_y$. With my system, the factors and their location in each of the chromosomes are seen at a glance. As the charting of autosomes progresses, their factors could be represented in the same manner, e.g. $I_{thl}II_{bcd}$, etc. and the factor-set of a diploid type by $I_{tthhll}II_{bbccdd}$, this latter example corresponding to a homozygotic individual. In consequence, I would first of all change Aida's denomination, $R_x r_y$, into $X_R Y_r$.

Furthermore, Aida has chosen R to represent the factor for the red colour, as most geneticists would have done, and r for the recessive allelomorph of this factor, whereas it would have been more descriptive to denote the factor for red by r (or R) and its absence by O; whether R or r should be chosen, would depend on whether red is dominant or recessive in relation to the normal type. My reason for choosing O to denote the absence of the colour-factors is that precisely the study of *Lebistes* (and *Aplocheilus*) very decidedly tend to bring about the conception that, whichever be the colour-factor considered, its allelomorph will be equal to O, i.e. that the corresponding gene is missing in the "recessive" type or is, in any case, inactive.

I have shown that, as crossing-over takes place between them, the X- and the Y-chromosomes are partners to the same extent as the other chromosomes in *Lebistes*. According to the current notion, each factor in the Y-chromosome should therefore have a corresponding allelomorph in the X-chromosome, and vice versa. Thus, the factors which I have called *m*, *i*, *f*, *r*, *s* and *e* should all have their corresponding allelomorph factors in the chromosome partner; but we have seen in the crossing experiments that whether we take a female in which *m* is lacking, or one in which *i* is lacking—i.e. whether the female belongs to the "Spot Race" or to the "Old Race"—it contains the same factors, that is to say *none* (X_oX_o) from the accountant's point of view, as far as colour-factors are concerned, or, in other words, only inactive or neutral genes. According to the current mode of denomination, my *Lebistes* females

should, in one case, have the formula $X_m X_m$, i.e. those of the "Spot Race," where the males should be called $X_m Y_M$; but if belonging to the "Old Race," their formula would be $X_i X_i$ and that of the males $X_i Y_I$; but whether we use the females of one race or the other, the result is exactly the same: the two kinds of females are identical as to inheritance, i.e. they are $X_{mi} X_{mi}$, a formula which is in so far irrational as $m = i$ and equal to all the other "recessive" allelomorphs, which are all equal to O.

This discussion touches the question of the right conception and denomination of genes or factors, and much would undoubtedly be gained if a uniform mode could be agreed upon.

In *Drosophila*, the organism which has hitherto been the most extensively studied, the "Normal Type," i.e. the wild type, is the established base upon which the whole terminology of factors has been built up. When forms appear, which are recessive with regard to this base, they are denoted by the corresponding small letters, while new dominant forms are denoted by capitals.

In *Antirrhinum*, there is no such decidedly normal type to refer to, and we might say that, here, the denomination of factors generally refers to an entirely recessive type.

In reality, the results are alike. In both organisms, the value of the factors is established in relation to a given type of fixed habitus or—in case the entirely recessive type is not viable—in relation to a type, the aggregate characters of which have been determined theoretically.

It makes no difference whether the type in question is measured or characterized in comparison with a wild type, chosen as "normal," or with an entirely recessive type. In both cases, the notation is relative, because it implies reference to a type, an individual of the same species, with which all other types are then compared.

Genetical science does not seem to take any interest in the systematic basis of the species as such. But we should say that this is an appearance only.

The present system of denoting factors—or rather pairs of factors—unavoidably presupposes that all types belonging to a species possess the same number of genes: any type must either possess the recessive or the dominant allelomorph of any pair of factors.

On reconsideration, this is a rather curious idea, which immediately calls forth the question as to whether all the species of a genus, all the genera of a family, etc. also have the same number of genes. Logically, and from a formal point of view, this hypothesis need not yet run against any self-contradiction. Taking *Antirrhinum* as an instance, and F to

stand for the red of its flowers, there could be no objection to the use of *ff*, not only for all ivory-coloured *Antirrhinum*, but also for all white peas or all animal organisms; for, in fact, none of the latter possess the predisposition to red of the *Antirrhinum* corolla. This, precisely, shows that, in the study of inheritance, the tendency to formalism is becoming rather pronounced.

There is hardly any reason whatever to suppose that two different varieties possess an equal number of inheritance-elements, i.e. genes. Even as the different species of a genus may hold chromosomes of entirely differing number and aspect, and therefore—if our conception of the genes, as arranged along the longitudinal axis of the chromosomes, is to hold at all—must have a widely differing number of genes, so it must no doubt also apply to the varieties within the species, that they need not contain the same number of genes.

The mistake we make in continually considering the number of genes as constant and identical in all related (and unrelated) organisms, very likely derives from the fact that our conception of the allelomorphs is somewhat erroneous and that, in principle, we must revert to the old presence-absence theory which, alone, explains why a type, a variety, a species, etc. can hold certain genes that are entirely lacking in others, where not even a corresponding gene-partner is found.

Not only in this connection do we get the impression that the presence-absence theory holds good. This applies to almost any genetic question. Of course, it makes no great difference whether, to explain a recessive factor, we assume the existence of a gene which is, under all circumstances, *inactive*, or whether we simply deny the existence of any such gene. But I suppose that the distinction between non-differentiating and differentiating elements really ought to find its expression by attributing the denominating "genes" exclusively to the latter, while the former should, from a genetical point of view, be represented by zero (0), as having no traceable influence on the sum of inherited elements of the organism. In reality, it is perhaps unessential whether the factor-denomination is assigned to the dominant or to the recessive allelomorph (its partner being put equal to 0). At any rate, it will not always be possible to decide which one of the two allelomorphs should have the factor index. It seems natural, however, as all recessive allelomorphs, as *m*, *i*, *f*, *r*, etc., have the same indeterminate value, to give them the value zero; in fact there is no difference between them, neither relatively nor absolutely. Although the study of inheritance essentially concerns relativity and fundamental *differences*, the real and, to my

mind, indispensable basis, would be generally to take 0 as the value of the recessive factors or genes and to count with positive values of recessive factors or genes only in such more rare cases as, for example, multiple allelomorphs. Referring to the latter case, one could imagine some slight shift in the chemical nature of the gene—provoking a special activity of each of the allelomorphic genes—to be the cause of the appearance of multiple allelomorphs; and in the first case, a shift in the chemical nature of the gene, to such an extent that the gene entirely lost its differentiating influence on the type.

In spite of this opinion, I have no doubt but that it would generally be inconvenient to apply another mode of denomination to the factors, than the present one. Zero as an index for the lack of a factor, would often be less suitable than a small letter, partly, because one is not always able to decide whether an allelomorphic factor is really missing in the case under consideration, partly, because the use of a small letter would often give a clearer formula. On the other hand, it would be convenient, when comparing to a "normal type," to be able to symbolize the factor, characterizing a different and recessive type, by a small letter, for instance *a*, the allelomorph of the normal type being here equal to 0, and to symbolize the factor of a dominant type by a capital letter, say, *B*, the allelomorph of the normal type being again 0.

Although, for my work on *Lebistes*, I have tentatively used a mode of denomination which was, in my opinion, more correct than the one used hitherto, I am quite aware that this method might cause some inconvenience in certain cases. The future must decide upon the system to be preferred.

As said before, there can hardly be any question of dominance or recessivity as far as the colour-factors in *Lebistes* are concerned. In the female, no colour-factor whatever can be traced; and in the male, when comparing to *Drosophila* conditions, even recessive factors would evidently appear and, *a fortiori*, the dominant ones. As however, at variance with *Drosophila*, crossing-over between the *X*- and the *Y*-chromosomes is possible in *Lebistes*, we might say that the colour-factors dominate their recessive allelomorphs but, as the latter are equal to 0, the index for dominance does not mean very much in this connection, as in many others;—it would simply mean that the gene, if present at all, manifests itself phenotypically in the male.

Considering the sex-factors in *Lebistes*, it is *possible* that real allelomorph factor exist, i.e. the male and the female factors, although we might conceive that, here again, the male sex-factor alone acts positively,

whereas the female factor is 0, i.e. does not alter the female character in the male direction.

It will be one of the tasks of the future to determine the dimensions of the genes. By calculating the percentage of crossing-over in *Drosophila*, the location of a great many of its chromosome-factors has already been charted, taking it for granted that the cross-over percentage may still be considered mainly as some function of the distance separating said genes along the longitudinal axis of the chromosome. The dimensions of the chromosomes being known, as well as the number of factors recorded and the relative distance between these, one may vaguely conceive the smallness of the units of measurement which will have to be used in connection with the genes. Probably, the length of chromosome to be considered in such calculations should be that characteristic of the synapsis stage, or an adjoining stage; it is probable that the genes of the chromosomes we observe, for example during the heterotypical division, are not strung along a straight line, but bunched like the beads of a row, kept in a wide test tube or the like. Unfortunately, the length of the chromosome at the stage of synapsis cannot be easily measured; a rough estimate will, however, show that we are still far from dimensions as for instance those of the molecules of albumen.

Even from a slight crossing-over as, say, 0·2, between two strongly-linked genes, we can conclude nothing as to the size of the genes, for two genes may of course be in close vicinity, whether they are large or small. It is necessary to know at least three neighbouring genes before being able to estimate the dimensions of the space occupied by the middle gene,—and it would be important that more observations be made of such strongly-linked genes, for the furtherance of the knowledge of the size of the genes. By the way, we do not know whether the genes take up the entire length of the longitudinal axis of the chromosome.

Sex-Linked, Sex-Limited and One-Sided Inheritance.

As a contribution towards the adoption, in scientific literature, of uniform terminology for the various modes of inheritance (at present, such terms as "sex-limited" and "sex-linked" are often used at random), I would point out that the denomination "*sex-linked*" (geschlechtsgebunden) ought to be applied only to conditions of inheritance explainable by the presence of the factor in question in those sex-chromosomes which are normally found in individuals of both sexes (*X*- and *Z*-chromosomes). "*One-sided*" (einseitig) inheritance should be used

only in such cases where the factor in question has its seat in that sex-chromosome which is normally found in one sex alone (*Y*- and *W*-chromosomes), adding the mention *male* or *female* so as to specify whether said factor belongs to the *Y*- or to the *W*-chromosome. The value of this distinction is not lessened by the fact that crossing-over between *X*- and *Y*-chromosomes has been proved, for nothing opposes the notion that, through a genetic displacement, one mode of inheritance may change into another. As to the denomination "*sex-limited*" inheritance, we are less fortunate because the secondary sex-characters, to which the term is generally assigned, are usually due to autosome-factors which, however, produce an exclusively *phenotypical effect* in individuals of one of the sexes. The milking capacity in cattle, the production of lupuline in hop, are instances of so-called (female) sex-limited inheritance. In reality, it is not a question of any special mode of inheritance, so far as we know, but only of phenotypical differences dependent on sex-determination. For this reason, the expression "sex-limited inheritance" is not very judicious in any case. "Sex-limited manifestation" would be better. "Phenotypically sex-limited inheritance" might perhaps do.

RÉSUMÉ.

A factor *e* (*elongatus*), involving an elongated caudal fin in male individuals of *Lebistes reticulatus*, shows sex-linked inheritance, for which reason the *e*-factor must have its seat in the *X*-chromosome of the male.

Crossing-over between the *X*- and the *Y*-chromosome is recorded, the *e*-factor thereby being transferred from the *X*-chromosome to the *Y*-chromosome. Males having thus their *e*-factor in the *Y*-chromosome, show one-sided male inheritance of the elongated tail fin.

In these cross-over males, having the *e*-factor in the *Y*-chromosome, a new crossing-over may take place between *X* and *Y*, so that the *e*-factor returns to the *X*-chromosome, and so on. The mode of inheritance is therefore continually oscillating between sex-linked inheritance and one-sided male inheritance.

The above shows that the *X*- and the *Y*-chromosome in *Lebistes* respectively contain a dominant male sex-factor and a recessive female sex-factor; also that this pair of factors is entirely like other pairs because its location in the chromosome is certain, and because it shows linkage to colour-factors, crossing-over, etc. In the above respects,

the divergence from conditions in *Drosophila melanogaster* is rather striking.

The Presence-Absence Theory and an ideal terminology are discussed.

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