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ARE PARTICULAR CHROMOSOMES SEX DETERMINANTS?

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The past decade has witnessed greatly renewed interest in the problems of sex determination, due very largely to the study of hybridization and the broad application of the results. Concurrently the investigation of the germ cells has increased in amount in a geometrical ratio; never before have these cells so fully engaged the thoughts of biologists, and our knowledge of the complex chromosomal activities has increased to an extent unpredicted.

In particular have multiplied investigations of the modified chromosomes, now described in animals for the spermatogenesis in insects, araneads, myriopods, copepoda, Sagitta and birds; and for the oogenesis in echinoderms, the cat, and possibly some insects (*Pyrrhocoris*, *Gryllus*). Following the terminology given by me in 1906, these may be collectively named allosomes, a term more convenient than my earlier one of heterochromosomes, in contrast to the unmodified chromosomes or autosomes. They have received a great variety of names: accessory, special, lagging, heterotropic, sex chromosomes; idiochromosomes, microchromosomes, diplosomes, gonochromosomes, chromatin nucleoli, etc. Any body within a nucleus that stains like chromatin should not, however, be considered an allosome until its chromosomal nature be ascertained.

Within the past eight years an hypothesis has arisen ascribing sex-determining properties to these allosomes, and my object is to treat this hypothesis first historically, and second critically.

A. The Hypothesis.

The first statement of the hypothesis is due to McClung in 1902, after investigation of the unpaired accessory chromosome in the spermatogenesis of Orthoptera — that kind of modified chromosome named by me in 1906 the monosome. McClung's conception of the function exercised by the accessory chromosome is "that it is the bearer of those qualities which pertain to the male organism, primary among which is the faculty of producing sex cells that have the form of spermatozoa." He recognized also that there must be selective fertilization, that to the ovum "come the two forms of spermatozoa from which selection is made in response to environmental necessities." At that time nothing was known of the maternal chromosomal number, so that it was natural for McClung to reason that the monosome was a paternal chromosome not represented in the female.

In the same year Sutton (1902) described for *Brachystola* that "twenty-three is the number of chromosomes in the male cells, while twenty-two is the number I have found in the female cells, and thus we seem to find a confirmation of McClung's suggestion that the accessory chromosome is in some way concerned in the determination of sex." Subsequent studies have shown that Sutton was wrong in his count of the oogonial chromosomes.

Then Stevens (1905) found in *Tenebrio* "that in both somatic and germ cells of the two sexes there is a difference not in the number of chromatin elements, but in the size of one, which is very small in the male and of the same size as the other nineteen in the female. . . . The small chromosome itself may not be a sex determinant, but the conditions in *Tenebrio* indicate that sex may in some cases be determined by a difference in the amount or quality of the chromatin in different spermatozoa." In 1906 she wrote: "The scheme also assumes either selective fertilization, or, what amounts to the same thing, infertility of gametic unions where like sex chromosomes are present"; and in 1909*a*: "The only other alternative in these insects seems to be that sex is already determined in the egg before fertilization, either as a matter of dominance, or as a result of maturation, and that fertilization is selective . . . but any such general application is premature until adequate evidence is at hand to prove that the sex character is represented in the chromosomes." Yet in another paper (1909*b*) that appeared simultaneously, Stevens writes: "As to the fact that the lagging chromosome of the aphids is a heterochromosome intimately connected with the phenomenon of sex determination, the present investigation of the male germ cells, I think, leaves no doubt."

Independently of Miss Stevens, and simultaneously, Wilson found that where there is a single monosome in the male, it is represented by a pair in the female; and where a large and small idiochromosome in the former, there is a pair of large ones in the latter. In his first two studies (1905*a*, *b*) he expressed himself guardedly as to such chromosomes being associated with sexual phenomena. In his third study (1906) he gives a much fuller discussion, and it is this treatment more than any other, that has aroused general interest in the subject. He mentions as one alternative that merely quantitative difference in amount of the chromatin may be the determining factor, but he criticises this for the reason that in *Nezara* the idiochromosomes are of equal size in both sexes, while a series of intergradations are known between such a condition and the one where these elements are dissimilar in size in the sexes. Therefore he maintains the alternative view, that the allosomes have qualitative differences that are sex-determining, with Mendelian dominance, and with selective fertilization. "The general interpretation . . . must include the assumption that there are two kinds of eggs (presumably in approximately equal numbers) that contain respectively the male and the female-determinant, and that the former are fertilized only by spermatozoa that lack the heterotropic chromosome (*i. e.*, the male determinant) and *vice versa*. . . . Such a selective fertilization is therefore a *sine qua non* of the assumption that the heterotropic chromosome is a specific sex-determinant." In this argument Wilson makes use of Castle's (1903) hypothesis that sex follows the rule of Mendelian segregation and dominance. To this view he adheres also in his fourth and fifth studies (1909*a*, *b*). But in his last paper (1909*c*) he opposes the Mendelian interpretation, because selective fertilization is improbable. He brings as another objection the case of the bee; here the egg after two maturation divisions forms a male if not fertilized, a female if fertilized; under the hypothesis the female tendency should be derived from the spermatozoon—"a *reductio ad absurdum;* for the male is derived from an unfertilized egg which has by the hypothesis eliminated the female tendency."

Nowlin (1906) and Boring (1907) analyzed the phenomena of the allosomes in Hemiptera and Coleoptera respectively, and Jordan (1908) in an orthopteran, all comparing chromosomal numbers in the female and male cells, and all inclined to regard the allosomes as sex-determinants. Morrill (1909) found that in *Protenor* and other species all the cleavage cells of one individual have either thirteen or fourteen chromosomes, *i. e.*, all either a single allosome or a pair, conformable with Wilson's results on the germ cells.[1]

Payne (1909) has accepted Wilson's views of a qualitative sex-determination by allosomes; while von Baehr (1909), in discussing the subject at length, is inclined towards the quantitative explanation. Wallace (1909) concluded that in *Agelena* some spermatozoa have two allosomes, others have none, and argued that a male would result when an ovum is fertilized by a sperm with these two elements; it should be noted, however, that the different describers of aranead spermatogenesis have reached quite conflicting results.[2]

Baltzer (1909) on echinoids, drew attention to the occurrence of allosomes (idiochrosomes) in the female line, though he studied the chrosomomes only in the pronuclei and cleavage cells, not in the growth period of the oöcytes. "We distinguish accordingly two types of eggs: some with and some without an unpaired element. The chromosome number is in both cases eighteen. Therefore, we must conclude that the unpaired chromosome in the egg type where it is wanting is represented by a rod-shaped element. The sperms—always with eighteen elements—are all alike. According to the discoveries on insects, it is not improbable that the determination of sex, which would lie with the female, is connected with this difference of the egg nuclei."

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[1] Some writers have denominated this case "*Wilson's Protenor-type,*" evidently ignorant that the spermatogenesis of this form was rather fully described by me (1901) some years before Wilson published his studies.

[2] Cf. the papers of Wagner, Berry, Bösenberg and myself.

Boveri (1909*a*) refers to Baltzer's work as indicative of sex-determination by particular chromosomes (the short hook-shaped ones). But in opposition to Wilson's explanation, he does not believe that one chromosome has a male and the other a female tendency, but that they differ only in activity: the larger allosome would give to a cell a larger power of assimilation, and such a view "would perhaps be qualified to serve as a basis for a general theory of sex-determination." Boring (1909) described the occurrence in the eggs of *Ascaris megalocephala* of a fifth, small chromosome element, but was unable to decide whether this is "a chromosome unit in itself, or a fragment of one of the long chromosomes," and considered it merely possible that it might be sex-determining. Boveri (1909*b*) holds this occasional structure to be undoubtedly sex-determining, a chromosome unit that is in most cases attached to the end of one of the others. At the same time he reports the occurrence of a monosome in the spermatogenesis of *Heterakis*, and concludes, in the sense of Wilson: "Fertilization of an egg by a sperm with five chromosomes leads to development of a female, by a sperm with four elements to production of a male."[1]

Finally, in the last paper on this subject, Edwards (1910) describes allosomes in the spermatogenesis of certain individuals of *Ascaris megalocephala*, and does not hesitate to call them sex-determinants.

B. Previous Criticisms of the Hypothesis.

In the preceding lines we have endeavored to state, in all brevity, the nature ofthe arguments advanced to prove that particular allosomes produce one sex or the other by their presence or absence,whether by qualitative or quantitative differences. Now we may consider certain objections that have been raised to such interpretations.

I have remained skeptical with regard to these hypotheses, though I have described many cases of allosomes in a succession

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[1] On p. 135, Boveri refers to "his" discovery in 1904 that "the tetrads of the first oöcyte division of *Ascaris meg. bivalens* can consist of two shorter and two longer rodlets," whereas this was (1904) particularly described and figured by me earlier in the same year.

of papers, and have expressed myself only once on the matter, in 1906, in considering Wilson's contention which I regarded "a very plausible conclusion, but there are in particular two phenomena which must be explained before it can be accepted. One is, how an allosome becomes lost in the spermatogenesis; and the other is, how the allosomes introduced by the spermatozoön into the ovum behave during the ovogenetic cycle; on both of these questions we know as yet practically nothing."

Gross (1904) objected to the hypothesis of McClung, (1) that it is not proven that accessory chromosomes are absent in females, and (2) the case of the bee, where males develop from unfertilized eggs. He also believed that the spermatozoa with monosomes may be incapable of fertilization; but failed to note that such supposition could not be applied to sperm with idiochromosomes.

Foot and Strobell (1909) urged that the theory of the individuality of the chromosomes is not proven—today, a decided minority view. They also held that the allosomes of *Euschistus* are not chromosomes at all, and are variable in number, which is in direct opposition to the discoveries of Wilson and myself. "In the case of *Euschistus* we are told that the larger of the two chromatin nucleoli of the spermatocyte is the homologue of the accessory chromosome of other forms, and if this interpretation is correct we may expect to find a large bivalent or two univalent chromatin nucleoli in the growing oöcytes." But they find no such bodies in oöcytes, and therefore conclude that the chromatin nucleoli of the male are never transmitted to the egg, are not chromosomes at all, and hence cannot be sex-determining; this objection to the Wilson-Stevens theory is inadmissible.

An explanation suggests itself to me why allosomes, which all evidence leads us to believe must be transmitted to eggs by fertilization, act in a different way in the oögenetic cycle. That is, in spermatogenesis the single monosome, or the pair of unequal idiochromosomes, behave differently from the other chromosomes, remaining dense and compact in the growth period of the spermatocytes, probably because they are there unpaired (monosome) or of unequal size (idiochromosome), while all the other chromosomes are paired, and the two of each pair seemingly alike. In the growth period of the oocytes, on the contrary, the allosomes of the spermatocytes seem to be represented by a pair of elements similar in all respects to each other; there is no dissimilarity of the pair, hence no conspicuous behavior different from that of the other chromosomes (autosomes). In other words, it is the singleness of the elements (monosomes), or their disparity in size and activity (idiochromosomes), that may be a reason why the allosomes behave so peculiarly in spermatogenesis. For these various considerations the arguments of Foot and Strobell against the hypothesis are not valid, though these investigators are quite right in seeing the necessity of comparing the oögenesis.

Buchner (1909) has entered other arguments against the determination of sex by allosomes, an hypothesis that he wholly rejects. He refers to their limited occurrence, which shows they could not be universal sex-determinants. Then to the occurrence of an accessory chromosome in the oögenesis, paralleling that in the spermatogenesis of *Gryllus*, he calls particular attention, insisting that it is necessary for the Wilson-Stevens theory that sperm-cells alone should have allosomes. "In *Gryllus* there can be no talk of a sex-determining function, and thereby naturally also not in the other animals with accessory chromosomes."[1]

Gutherz (1909) has, however, combated Buchner's opinion that the chromatic body in the oöcytes of *Gryllus* is a chromosome, and shows that it differs from such in many details. He also finds that "the diploid chromosome group of the male numbers 21, that of the female 22 chromosomes." "The doctrine

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[1] There are a couple of points in which Buchner seems to be in error. He states (p. 409) that Goldschmidt had argued in 1904 that the allosomes might represent "trophic chromatin," and accuses me of having in 1906 overlooked Goldschmidt's priority. As a matter of fact, I wrote in 1901: "Thus it might be that in the insects the chromatic nucleoli are those chromosomes which either exert a greater metabolic activity than the other chromosomes, or which carry out some special kind of metabolism." It was Goldschmidt who had overlooked my earlier statement of this view. Then on p. 415, Buchner concludes that "the accessory chromosome (monosome) is no unit body, as has been generally assumed up to this time, but a bivalent with non-equivalent components." But in 1901, and again in 1905, I argued that the larger monosomes of sperm cells may be bivalent elements, the pair that is separate in the oögenesis represented by a pair in fusion in spermatogenesis.

of the connection between heterochromosomes and sex-determination is accordingly not disturbed by this discovery."

Morgan (1909, 1907) classes the theories of sex determination by chromosomes as qualitative and quantitative, and inclines to the latter view—he being the first to take this stand positively. By a quantitative interpretation he does "not mean that the female is simply male plus something else, a view recently advanced by Castle, but that male and female are two alternate possibilities of the living material, which possibility is realized depending on quantitative factors. . . . The gametes are not, therefore, male and female, but contain certain factors which, when combined, give rise, in an epigenetic fashion, to one or the other alternative." In the phylloxerans, the "loss of certain chromosomes from the male egg appears to follow, not to precede the size relation. . . . But there is nothing in these facts that shows that the effects are directly quantitative rather than that observable quantitative differences accompany, or follow in some cases, more profound changes." He considers as the most serious objection to the qualitative interpretation "that although the hypothesis is ostensibly based on the presence of certain chromosomes which are assumed to be male and female determining respectively, yet to these chromosomes, which are to all appearances identical, are ascribed exactly opposite functions." Morgan's whole attitude is rather hostile to the view that particular chromosomes are sex-determinants, and his arguments against the view are the most cogent yet presented.

C. Further Criticisms of the Hypothesis.

In a previous treatment (1906*a*) of the phenomenon of sexuality, I was led to define it (p. 85) as "essentially the condition of difference obtaining between conjugating individuals. . . . Because conjugation is a process distinct from reproduction, sexuality, being intimately associated with conjugation, has no primary connection with reproduction. . . . The genesis of sexuality has been this: that out of a state where all individuals were equally capable of reproduction a condition of division of labor has ensued, inducing morphological and chemical differences, between individuals capable of reproduction and conjugation and other individuals capable of reproduction and conjugation alone. This holds true in the Metazoa, both for the germ cells and for the persons, and the male is characterized by his power to conjugate or fertilize, the female by her power to reproduce. A microgamete in the Protozoa, or a spermatozoön or male person in the Metazoa, is an individual that has lost the power of reproduction in becoming specialized for the act of conjugation. Sexuality is then the state of occurrence of dissimilar conjugating individuals, and the essential point in this dissimilarity is that only one kind of these individuals has the power to reproduce. This simple interpretation was entirely overlooked by Geddes and Thomson in their theory of 'The Evolution of Sex.' ".

The germ cells are then not without sex, as Morgan would have us believe, but have an actual *sexuality* with respect to each other, an ovum being female and a spermatozoön male; as well as a *prospective* sexuality with regard to the kind of individual they may engender. We are here concerned with the question of the determination by particular chromosomes of prospective sexuality.

Further, a hermaphrodite is bisexual, and its egg therefore prospectively bisexual, engendering both kinds of gametes. This indicates that an egg may contain potentially the characters of both sexes, or better stated, that both states of sex may arise from the same egg. This may also be true for species that are not hermaphrodite, for a female individual frequently shows certain male characteristics, and a male certain female qualities, even if in a more or less latent condition. These conditions indicate that an egg does not contain prospectively one sexual state to the exclusion of the other, but rather that maleness and femaleness are closely associated phenomena that may interchange within the same individual; a possibility suggested by Morgan (1909).

Bearing these ideas of the value of sex in mind, the following main objections may be made to the hypothesis that particular allosomes act as sex determinants:

1. While the phenomena appear to admit of a simple explanation in cases where there are only a pair of idiochromosomes, or a single monosome, in the spermatogenesis, often the conditions

of the allosomes are so much more complex than this, allowing so many different chromosomal combinations in the spermatozoa, that the interpretation of what spermatozoa are male-producing and what are female-producing becomes very difficult. Attention may be drawn, for example, to a case in the Hemiptera described by me (1901, 1906*b*). In spermatocytes of *Calocoris rapidus* there are: "twelve autosomes that divide in both mitoses, two diplosomes that do likewise (therefore are probably also bivalent), a smaller monosome that does not divide in the first but does divide in the second mitosis, and a larger monosome that divides in the first but not in the second mitosis." Other complex associations of allosomes have been described by McClung and Payne. Were the allosomes sex-determinants, we would have to conclude that in certain species a considerable number of the chromosomes subserve this end, which would be allotting an undue amount of the nuclear material to this purpose.

2. In all plants, with the exception of one (*Salomonia*) described by Cardiff (1906), and in may animals, no allosomes are known, yet these species have sexuality. It is probable that such structures will be found in certain cases where they have may been overlooked; yet they are apparently absent in some cases where special search has been made for them; accordingly, at the most they can be sex-determinants in only a limited number of cases.

3. In certain species there is the phenomenon of two sizes of eggs, some larger that produce females, others smaller and male-producing. This is known for the Phylloxerans, Rotatoria and *Dinophilus apatris;* another case has been described for an acarine by Reuter (1907); and I have shown (1907) that there are two sizes of eggs in the aranead *Theridium*, though I did not raise these eggs to determine their prospective sex values. These two kinds of eggs may be produced by the same individual, or (Rotatoria, Punnett, 1906) by different individuals. These eggs become distinguishable in the growth period, and for the Phylloxerans Morgan (1909) has shown that the egg is "sexually determined" before the formation of the polar bodies. Malsen (1906) held for *Dinophilus apatris* that the "difference between male and female eggs apparently lies chiefly in the greater or less number of fusing ovogonia"; but his brief description and few figures do

not prove this point. But however these differences arise they are clearly present early in the growth period, which is strong evidence that they cannot be produced by any sorting of allosomes in fertilization. And it is quite possible, as Beard has reasoned, that a distinction of male and female eggs may be a general phenomenon, though not usually associated with dimegaly.

4. In parthenogenesis sex is necessarily determined without fertilization; from such eggs of Rotatoria, aphids, Phylloxerans and daphnids both males and females develop. Since there is no fertilization the daughter individuals should have the same chromosome complex as the parent, should all be females, were sex determined by particular chromosomes. Else there should be anticipated separations of particular chromosomes in definite manners, which would seem to imply most complex mechanical movements; as yet we know nothing definite of such movements.

5. In hermaphroditic species an egg gives rise to a bisexual individual, never to a unisexual. Were there sex determination by particular combinations of allosomes in the fertilized egg, we would necessarily expect occasional unisexual individuals to result. In *Sagitta* Stevens (1905) found an allosome in the spermatogenesis, but neither in oögenesis nor in the first cleavage; and she, as Cardiff (1906) who described one in the plant *Salomonia*, points out that such an element can have no sexual value in these hermaphrodite species.[1]

6. As Wilson and others have realized, to regard particular allosomes as direct sex-determinants logically necessitates selective fertilization. Until a case of selective fertilization has been demonstrated, however, the discussion on this point had better be tabled.

7. Morgan has urged that it may be the mass rather than the quality of the chromosome substance that may be sex-determinative, provided that such substance is determinative at all. It is the general rule in insects that the male has less chromosome substance than the female, in having a single monosome, or a small and large idiochromosome in the place of two large ones. It might then be argued that such allosomes, by the difference in mass which they occasion, establish the prospective sex value.

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[1] It is not actually proven that these bodies are of chromosomal nature.

This agrees with the fact that eggs which have given off both polar bodies and are not fertilized give rise to males, as in the Rotatoria (Whitney) and some Hymenoptera.[1] However, this does not necessarily imply that particular chromosomes are sex-determinative even quantitatively, but that the mass of all chromosomes collectively may be determinative.

8. The hypothesis neglects the part that other substances, such as the cytoplasm and the mitochondria, may have in sex determination.

9. The strongest objection to the hypothesis of particular chromosomes being specially sex-determinative remains to be discussed, and it may equally well be made against certain current explanations of heredity in general. There can be little question, at least in the present state of our understanding, that chromosomes are of great importance in cellular metabolism, and even evidence that they are in part enzyme masses. But these chromosomes, while preserving their continuity from generation to generation, which I hold to be abundantly established, are in no sense independent units, but parts of a larger whole, the "nuclear element," composed of the sum of the chromatin and linin. Further, this nuclear element is not an independent unit, but only a part, even if it be the most important part, of the cell whole. Thus the idea is erroneous to speak of the chromosomes as automatic units, for they are but parts of the cell or cell complex. The whole, as Whitman (1893) argued, cannot be the single cells or parts of them, but the entire inclusive organization. For the organism acts as a whole, not simply as the sum of many parts; it is the interrelation of the activities of the many parts, added to these, that constitutes the behavior of this major unit.

Now to assume that particular chromosomes alone are sex-determinants is to disregard this complex inter-activity. At the

[1] It is now fairly well established that drones of the honey-bee, hornet, wasp and ant all possess the reduced number of chromosomes, and therefore must have originated from unfertilized eggs that had produced two polar bodies. The work of Meves (1907, 1908), Mark and Copeland (1906, 1907), Lams (1908) and Schleip (1908) is thoroughly corroborative of this conclusion. But this does not prove that in the Hymenoptera all unfertilized eggs give rise to males, for there seem to be certain established records of females resulting from unfertilized eggs, which cases have been collected from the literature by Wheeler (1903) and Shull (1910).

most we are justified in concluding only that the chromosomes have a share in the establishment of sex. He would be rash who would venture to claim that a particular chromosome determines excretion, another determines locomotion; yet these processes are relatively simple compared with that of sexuality, which some have contended may be controlled by a particular chromosome. The hypothesis is too naïve, it assumes too great simplicity of the cell, it tastes too strong of rigid predetermination.

The idea of unit characters, promulgated mainly by the work of Mendel, DeVries and their followers, is largely to blame for such hypotheses. It seems to me that physiological study has sufficiently demonstrated that there are no actual unit characters, and it is but natural that physiologists have refused to accept them. In the analysis of cross-breeding, the investigator has to focus his attention upon one or but a few characteristics of the organism; he has to close his eyes to the great multitude of characteristics, for they are too numerous for any one mind to grasp at once. The characters he may select for examination are his units of study, and he is entirely justified in speaking of them as unit characters, provided he does not forget that they are merely arbitrary units of convenience. But most hybridists have gone further than this; they have sought to directly compare such arbitrary excerpts with units of organization, scarcely pausing to consider what is a unit of organization. Surely it is the organism as a whole that is the only unit, and just as surely all its parts are most complexly interrelated. The living body is a unity, not a colony.

Modern Mendelian explanations represent a determinant theory far more rigid and complex than that of Weismann, though, strangely enough, most Mendelists in the inception of their studies were unsympathetic to Weismannian interpretation. This is the most curious instance of how men have come to identify an arbitrary term of convenience with a part of the living organization.

When Sutton (1903) pointed out that the paternal and maternal chromosome series parallel in their pairing and separation phenomena of alternative inheritance, thus seeming to present a cellular basis for Mendelism, and Castle (1903) argued that sex follows such inheritance, the thought originated of identifying unit characters with chromosomes. It was made to appear that unit characters are present in the germ, though just what relation a rose comb has to a particular chromosome was not elucidated. Such a concatenation of ideas as this naturally led to the identification of "sex-units" with certain chromosomes.

The better founded idea that the organism behaves as a whole, whether it be a germ cell or a multicellular body, should make us hesitate to localize any particular function solely in one particular structure, for that would mean to disregard the importance of interrelations of parts. Thus when we find particular chromosomes in one sex and not in the other, it by no means follows that these are the cause of the sex difference. All we can say at the present time is that the two phenomena are coincident. Thus I am inclined to agree with Morgan's (1909) closing thoughts: "The accessory (chromosome) may follow sex or be associated with other differences that determine sex, rather than be its sole cause."

In all probability the activities of the chromosomes are influential in establishing sex, but not in the crude way in which the process has been imagined.

One point is quite clear, that fertilization is not necessary for the establishment of sex, for any unfertilized egg that develops furnishes a sexual individual. At the same time sex may be changed by fertilization; thus Whitney (1909) has shown it to be probable that the male eggs of Rotatoria furnish males if not fertilized, but females when fecundated. Sex is then established before, but may be changed by fertilization. This clearly implies that maleness and femaleness are not unchangeable unit characters, as does also the fact that an individual of one sex may develop some of the characteristics of the other sex, a phenomenon so apparent in the human body. Maleness and femaleness would appear to be two modes of one process, the process of germ cell production, not radically different conditions. In other words, there is no valid reason to interpret sex as an immutable unit character resident in or presided over by particular chromosomes, and sorted out and distributed by Mendelian segregation with all the complex mechanisms of dominance and determiners; but rather as a growth, the result of a labile process which may be changed by a variety of influences.

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