falls short of the best attainable. The scholarly teacher, with the genuine passion for making scholars, is fortunate indeed if he combines with it such broad sympathy and good sense that his pupils will come to him for advice on homely, everyday questions; for the influence thus gained doubtless reaches farther than we can possibly know. For the teacher of science, who more than his colleagues in other departments of learning, has the opportunity to lead the thoughts of his pupils by an occasional judicious word toward a better appreciation of the orderliness of that which we do know, and of the vastness of that which is beyond our ken, the privileges as well as the responsibilities are especially great.

The teacher's career is one of some sacrifice. Let us admit it, and admit also that it may not be undertaken by those who have not aptitude and liking for it, for these are both indispensable to success. But let us remember, too, that it is truly a noble calling, accorded a dignified standing in our communities; that it means for those who enter upon it an association with scholars and a share in those affairs which we believe make for advancement of our race; that its rewards in the way of recognition among scholars, and in the occasional spontaneous expressions of appreciation on the part of pupils, as well as in the lasting friendships formed, are not unworthy to be placed beside the more striking and tangible financial successes of other professions. Let us recall that the advancement of our sciences must always depend in a large measure upon the maintenance of a high type of teacher, as well as of teaching, for which we need able, broad-minded men, not those who are merely indisposed to adopt some other profession; and to this end let us foster an interest in the teacher's career on the part of more of those to whom those traits of mind and character which make for success in this honorable profession have been freely given.

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RECENT RESEARCHES ON THE DETERMINATION AND HEREDITY OF SEX[1]

I. STATEMENT OF THE PROBLEM

DESPITE certain technical difficulties, the subject of sex-production has seemed to me to be an appropriate theme for this occasion for two reasons. The phenomenon of sex is so nearly a universal one that it may be assumed to make some appeal to the interest of biologists in every field of inquiry. Secondly, although the physiological meaning of sex still remains in many respects enigmatical, it may fairly be said that substantial advances in the analysis of the mechanism of sex-production are being made by experimental and cytological research. It is not my intention to consider at this time the possible significance of sexual reproduction or the physiological and cytological problems involved in the phenomena of fertilization. My discussion will be confined mainly to the more recent of the researches that have thrown light on the questions of sex-determination and sex-heredity. Does sex arise, as was so long believed, as a response of the developing organism to external stimuli? Or is it automatically ordered by internal factors, and if so, what is their nature?

It will be well at the outset to remove any possible obscurity from our definition of the problem. Every form of heredity —and sex-production, broadly speaking, is unquestionably a phenomenon of heredity —is in one sense a response of the developing organism to external stimuli. The

[1] Address of the vice-president and chairman of Section F—Zoology—of the American Association for the Advancement of Science, Baltimore, 1908.

characteristic mode of development of the organism (which is only another way of saying its heredity) is as definitely conditioned by its environment as by those internal agencies that we ascribe to the specific organization of the germ. The end result is a product of internal and external factors acting together. But the distinction I have drawn is nevertheless perfectly real and definite, as will perhaps appear more clearly if the inquiry is stated in the following way:

1. Is the germ originally of indeterminate sex, or sexless, being determined as male or female at some later period by corresponding differences of conditions external to the germ? Or,

2. Given an identity of external conditions in each case, is the germ predetermined from the beginning as male, female or hermaphrodite by internal factors of its organization? And

3. If such predetermination exists, what is its physical basis?

These questions can not be adequately considered without some preliminary examination of the sexual distinction in general. We use the words "male" and "female" in a double sense. In the original and still common one they denote certain characteristics of the individual body, primarily those shown in the reproductive organs, secondarily those of other organs. Later the same terms were often applied to the germ-cells themselves, the eggs being spoken of as the "female germ-cells," the spermatozoa as the "male"; and this usage is often met with at the present time, even in technical treatises. But confusion thus at once arises; for, as we shall see, there are many cases in which the eggs or the spermatozoa are themselves of two classes which are respectively male-producing and female-producing, and have accordingly been spoken of as "male" and "female." It is therefore preferable, at least in case of the higher organisms, to designate the gametes as paternal and maternal, restricting the words male and female to the body by which they are produced. In the case of unicellular forms, where every cell may be potentially or actually a gamete, it is doubtful whether the words male and female should be used at all. In the isogamous forms, some of which occur among the lower multicellular types, the gametes are of equal size and similar structure, so that every visible sexual distinction may vanish. But even here the gametes are in some cases known to be of two physiological classes (as in certain simple algæ and fungi) each of which unites only with the other. A primitive form of sexuality is therefore present, but the gametes and the individuals that produce them can only be designated by non-committal terms such as "plus" and "minus" (Blakeslee).

Even in the higher plants and animals caution is necessary in our use of terms. Primarily we designate as males and females individuals that produce respectively spermatozoa and eggs, or their analogues; and as hermaphrodites those that produce both kinds of gametes. In the flowering plants confusion arises from the transference of these terms by analogy to the non-sexual generation or sporophyte; and a species may be hermaphrodite or monecious in respect to this generation and diecious in respect to the sexual generation or gametophyte. But whether in this sense or in the original one the sex-distinctions are not fixed or absolute. Not infrequently in hermaphrodites the production of eggs and of spermatozoa takes place at different times, so that the organism passes through a functional male stage and a functional female one. Conversely, it is a familiar fact that the sexual characters of diecious forms are seldom completely separate. Each sex frequently

exhibits in a more or less rudimentary form characters that are fully developed and functional only in the opposite sex. In exceptional cases these structures may become fully developed or even functional, as we see in the occasional appearance of functional mammary glands in the male mammal, or of fully formed stamens in a female flower; while true hermaphrodites occasionally appear, even in diecious species. This suggests that "male" and "female" are but relative terms that denote tendencies more or less pronounced but not absolutely separate or distinct. The male or female has accordingly often been regarded as a potential hermaphrodite in which one sexual tendency dominates more or less completely over the other; though, as will be seen, there is reason to regard the distinction between hermaphrodite and diecious organisms as more fundamental than this. The sexual individual is thus in some respects comparable to a Mendelian hybrid; and a number of eminent students of the subject have endeavored to show that it actually is such a hybrid.

The past decade has witnessed a remarkable change of front in regard to the general problem. Even in very early times it was suspected that sex might be controlled by internal factors; and such has long been known to be probable in case of the honey-bee, where, if the Dzierzon theory be correct, the fertilized eggs produce only females, the unfertilized eggs, males. Until recently, nevertheless, opinion has been largely dominated by the view that sex-production is in general controlled by extrinsic conditions. A large number of the earlier researches, and some of the later ones, have in fact seemed to show that sex is thus determined. There is no manner of doubt that sex-production may be affected by such conditions, and that its operation may thus be in some cases artificially altered. A classical example of this is the fact, shown by the researches of Prandtl, Buchtien, Klebs and others, that alterations in the conditions of nutrition or of light may determine the production of the male and female organs in fern prothallia; and analogous effects of changed external conditions have been produced in case of Hydra. But these are not properly cases of sex-determination, but rather of the suppression or retardation of one set of sexual organs in favor of the other in hermaphrodites; and they are not to be directly compared to a change of sex in the true diecious forms. Again, it has long been known that the production of males in the aphids is definitely affected by external conditions, and more recent experiments show that the same is true of the daphnids. But here again we are not dealing with a change of sex in the individual. These effects involve a change from parthenogenetic generations that produce only females to those that produce sexual females and males. The same is true of Maupas's well-known results on the rotifer *Hydatina* (though these have been disputed). As far as ordinary diecious forms are concerned most of the recent experimental work, such as that of Strasburger on the flowering plants, of the Marchals on diecious mosses, of Schultze and Cuénot on mammals, insects, amphibia and other animals, has led to purely negative results, and seems to show that from the fertilized egg onward the sex of the individual is unalterable by external conditions.

II. SEXUAL PREDETERMINATION AND PREDESTINATION IN THE GERM-CELLS

The whole mass of statistical and experimental data on this question is placed in a new light by the proof, recently brought forward, that in many organisms the fertilized egg or zygote is already prede-

termined as male, female or hermaphrodite; while very many of the earlier experimental data have either failed of confirmation or have been shown to be susceptible of a different interpretation from that first assigned to them. Cytological and experimental research combine to show, not only that sex is predetermined in the zygote, but also that it is in many cases *predestined* (I do not here say predetermined) in the gametes or even much earlier. It is a familiar fact that in some of the higher pteridophytes sex is predestined in the microspores and megaspores which produce, respectively, male and female prothallia; and the same is, of course, true of their homologues in the flowering plants. It has likewise long been known that in a few cases sex is similarly predestined in eggs of two sizes in the animals, for instance in *Hydatina, Phylloxera* and *Dinophilus apatris*. But even in cases where the germ-cells appear quite alike to the eye it has been shown that a sexual predestination may exist. A primitive but perfectly definite predestination of this kind has, for instance, been proved by Blakeslee to exist in both the zygotes and the asexual spores of various species of fungi; and a similar predestination has been demonstrated also in some of the more highly differentiated types, such as the mosses and liverworts. As an example of this I select the recent beautiful studies of the Marchals on the diecious mosses. Isolation cultures prove that the asexual spores, though similar in appearance, are individually predestined as male-producing and female-producing; and all efforts to alter this predestination by changes in the conditions of nutrition, such as are known to be effective in the case of fern prothallia, failed to produce the least effect. Again, the remarkable experimental results of Correns on diecious flowering plants (*Bryonia*) prove that the pollen-grains, though apparently alike morphologically, are predestined in equal numbers as male-producing and female-producing. Half the pollen-grains upon fertilizing the eggs produce males and half females. In the mosses the Marchals demonstrate that all the products of a single spore are likewise immutably determined, since new plants formed by regeneration from fragments of the protonema or from any part of the gametophyte, are always of the same sex. Evidently, sex is here a quality that pervades all the cells of the organism, independently of the external conditions. These results tally with a considerable body of evidence on the zoological side that all the products of a single egg are of the same sex. This is shown, for example, by the similar sex of double monsters, and still more strikingly by that of multiple embryos derived from the same egg. The work of Bugnion, Marchal and Sylvestri has shown that in some of the Chalcidæ (*Encyrtus, Litomastix, Ageniaspis*) each fertilized egg produces large numbers of secondary embryos by an asexual process. All of those arising from a single egg are of the same sex—female if the egg be fertilized, male if it be unfertilized, as in the bee and ant.

III. Cytological Basis of the Sexual Predestination in the Air-Breathing Arthropoda

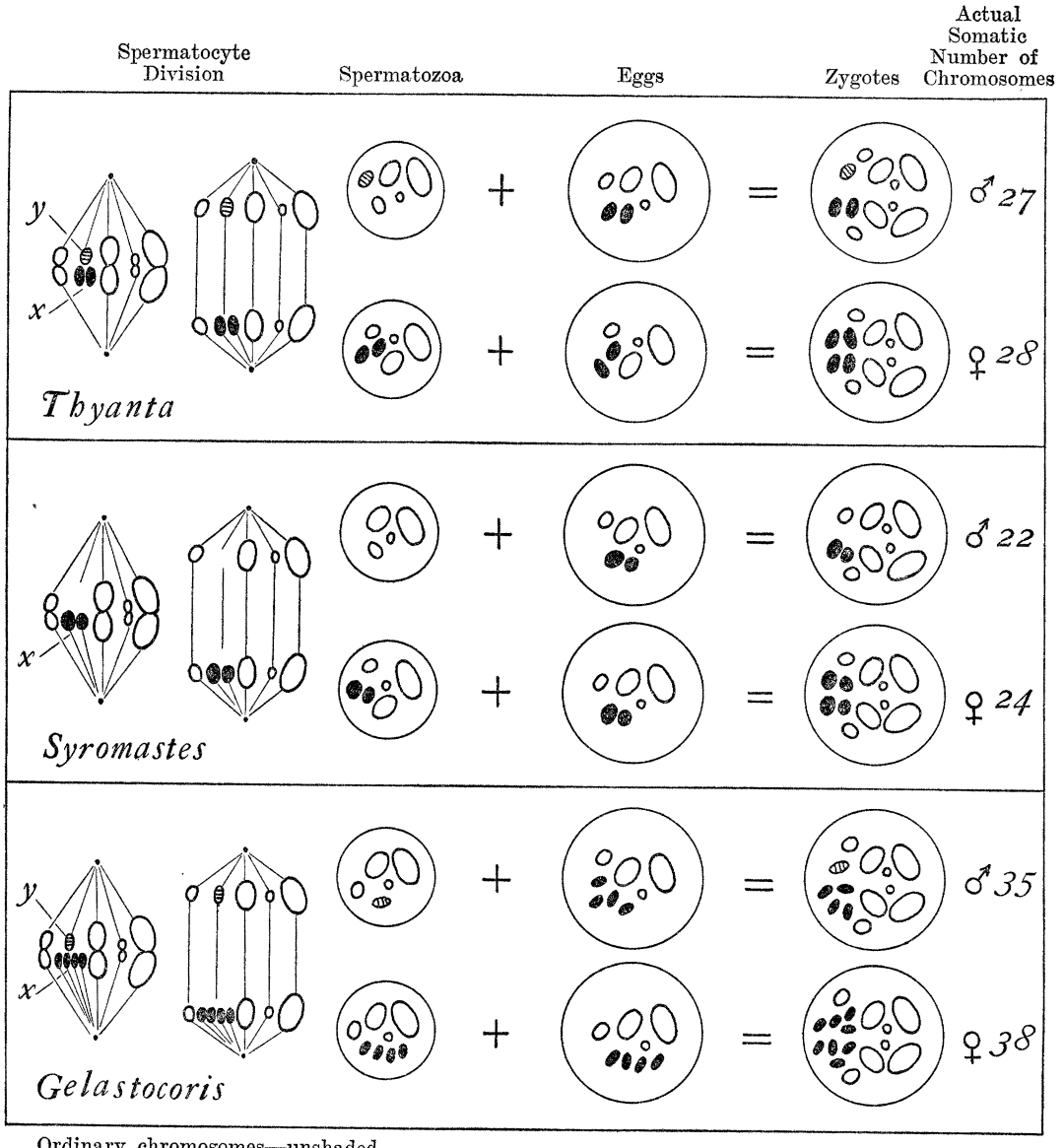
In none of the cases just cited is anything positively known of the cytological basis of the sexual predestination in the germ-cells. Our knowledge of this side of the question is thus far confined to three groups of the air-breathing arthropods, but we here find a substantial basis for a broader consideration of the entire problem. Cytological studies on insects, myriapods and arachnids have demonstrated that in many of these forms a sexual predestina-

tion is clearly shown in the nuclei of the spermatozoa, and in particular in the constitution of the chromosome groups. The spermatozoa are in fact of two classes, equal in number, that differ in respect to one or more of the chromosomes that enter into the formation of their nuclei; and the facts clearly demonstrate that fertilization of the eggs by one class produces males, by the other class females. This dimorphism of the spermatozoa was discovered by Henking as long ago as 1891 in the hemipteran genus *Pyrrochoris,* and was confirmed by Paulmier in *Anasa* eight years later, but neither of these observers suspected its meaning. Its significance was first suggested by McClung in 1902, but direct proof of the fact was first brought forward by Stevens and Wilson three years later in certain species of hemiptera and coleoptera. The result attained in these species has now been extended to nearly a hundred species of insects through the studies of a number of observers, among whom a group of American cytologists have led the way. In all these species sex-production conforms to a common principle, which has recently received a beautiful confirmation through the study of some of the parthenogenetic species; but there are many variations of detail, which have been so puzzling as to have caused many errors of observation and interpretation, and the literature of the subject has in consequence fallen into a bewildering confusion that is only now fairly being cleared away. I will state the essential facts as briefly as possible.

In all the species half the spermatozoa are characterized by the presence of a special nuclear element which I shall call the "X-element," while the other half fail to receive this element. In the simplest and clearest case (which was that first discovered) the X-element is a single chromosome, now generally known by the name of the "accessory chromosome," given to it by McClung, but it is also called the "odd" or "heterotropic" chromosome, the "monosome," or the "unpaired idiochromosome." I will here employ McClung's more familiar term. As a single accessory chromosome the X-element has been found in many representatives of the hemiptera, orthoptera and coleoptera, and in certain odonata, myriapoda and arachnida. The typical accessory chromosome has no synaptic mate or partner; and here lies the explanation of the fact that in the maturation divisions it passes into only half the spermatozoa.[2] In many cases, however, the X-element (otherwise identical with an accessory chromosome) appears as a "large idiochromosome" which has a synaptic mate known as the "small idiochromosome." This latter chromosome, or its homologue, I shall designate as the "Y-element." In a few cases the X-element consists of two chromosomes (*Thyanta, Fitchia*), of three (*Prionidus, Sinea*), or even of four (*Gelastocoris*), accompanied in each of these cases by a single Y-element. In *Syromastes* (at present a unique case) the X-element is double, but is not accompanied by a Y-element.[3] In all cases the spermatozoa are formed in pairs, and the chromosomes are so distributed in the maturation-divisions that one member of each pair receives the X-element (whether it consist of one, two or more chromosomes), the other member the Y-element if it be present. This is illustrated by the accom-

[2] The two members of every pair of chromosomes are separated in the reduction division and pass, respectively, into the members of a corresponding pair of spermatozoa. Hence the reduction of the original number to one half in each spermatozoon, and hence also the failure of one member of each pair of spermatozoa to receive the X-element.

[3] The cases of *Fitchia, Prionidus* and *Sinea* are reported from unpublished observations by Mr. F. Payne, made in my laboratory.

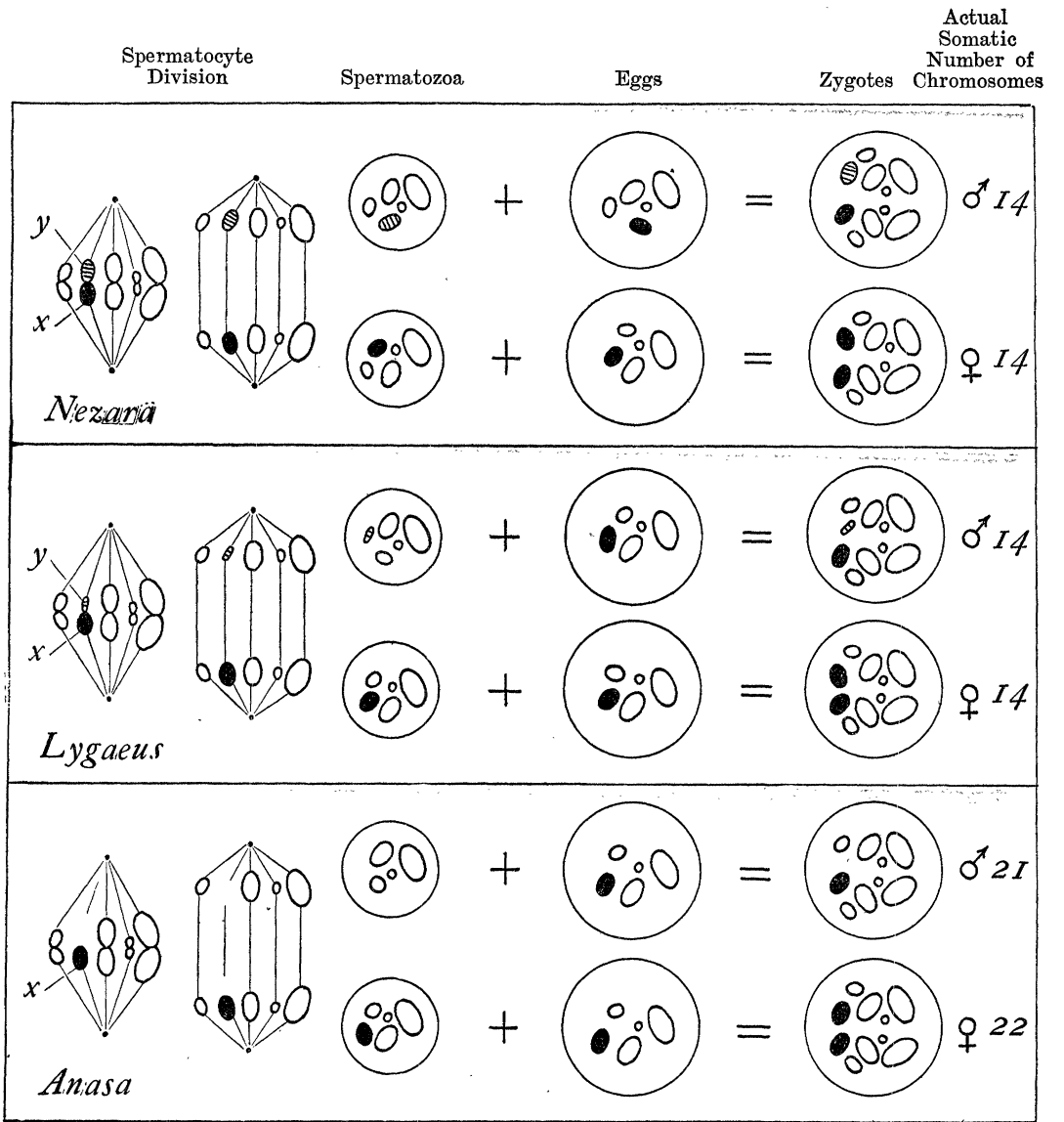


Ordinary chromosomes—unshaded.
x element—black.
y element—with cross-bars.

panying diagrams.[4] Half of all the spermatozoa thus receive the X-element, while the other half may receive a Y-element in its place, though this may be absent.

Comparison of the male and female somatic chromosome-groups proves, indirecting. The X-element is in each case black, the Y-element cross-barred. The actual numbers of the chromosomes are given for each sex at the right.

[4] These diagrams are from my own observations with exception of those of *Gelastocoris* (from Payne). For the sake of simplicity and ready comparison all the forms are represented with but four pairs of ordinary chromosomes (in white), all with the same size-relations and group-



Ordinary chromosomes—unshaded.
w element—black.
y element—with cross-bars.

ly, but conclusively, that the two classes of spermatozoa thus formed are, respectively, female-producing and male-producing (I do not say female- or male-*determining*), as already stated. In both sexes the somatic groups are identical save in respect to the X- and Y-elements; and the difference can only be a result of fertilization by the two respective classes of spermatozoa. This is at once proved in species having a Y-element by the fact that this chromosome is found only in the male. The evidence given by the X-element alone is equally decisive. This is present in both sexes, but,

whatever be its particular composition (whether a single chromosome or more than one) it is present as a single unit in the male, while in the female it is doubled. The explanation of this fact is as follows: It is true of organisms generally that in maturation each pair of chromosomes is reduced to a single chromosome. The X-pair in the female must, therefore, be reduced to a single X-element, which is present in all the eggs when ready for fertilization,[5] while in the male it is present in only half the spermatozoa. The characteristic female combination can, therefore, only arise by fertilization of the egg by spermatozoa that contain the X-element, as is shown by the following formulas:

(*a*) In the absence of a Y-element

Egg X + spermatozoon X = zygote XX (female)
Egg X + spermatozoon no X = zygote X (male)

(*b*) In the presence of a Y-element

Egg X + spermatozoon X = zygote XX (female)
Egg X + spermatozoon Y = zygote XY (male)

In either case it is evident that the X-element of the male zygote is derived from the egg. The significance of the Y-element is not known; but since it is often altogether absent, it apparently does not play a necessary rôle in sex-production, and may, for the present, be left out of account.

This general result has not been attained without many false steps which have confused the simple principle to which the phenomena conform; but so many of the contradictions have disappeared upon more exact later studies that we may now confidently expect to see the few remaining ones cleared away.

It is clear from these facts that the sexes often differ in the number of the chromosomes; and in this case it is always the female that has the larger number. When the X-element is a single unpaired chromosome in the male (accessory chromosome) the female has one more chromosome than the male (*Anasa, Protenor*). When the X-element in the male is double, but without a Y-element, the female has two more chromosomes than the male (*Syromastes*).[6] When a Y-element is present the numerical relations are modified accordingly (since this element is present in the male, absent in the female). Thus, in *Gelastocoris* the X-element is represented by four chromosomes in the male, while the female has eight; but since the male has in addition a single Y-element the net difference between male and female is but three. In the common case where the male contains a single X-element (large "idiochromosome") and a single Y-element ("small idiochromosome") the sexes have the same number, the female containing X + X and the male X + Y. In this case the Y-element may often be distinguished by its size and the male and female chromosome-groups are visibly different. In some cases, however, the Y-element is as large as the X-element (*Nezara, Oncopeltus*) and no visible difference between the sexes appears to the eye; but this case is connected by intermediate gradations in other species with cases in which the difference plainly appears, and we have every reason to believe that the same principle applies to all. The general formulas X + X = female and X + Y = male may, therefore, apply to many forms in which no nuclear differences between the sexes are visible.

The general conclusion reached by the study of the purely sexual forms has recently received a most convincing confirmation through the brilliant discoveries of Morgan and von Baehr on some of the

[5] This part of the conclusion, at first based on indirect evidence only, has recently been shown to be true by observations, still unpublished, by Mr. C. V. Morrill.

[6] The female number in this case, which I at first inferred only, has recently been demonstrated by direct observation.

parthenogenetic forms, which have hitherto seemed to constitute a serious difficulty. Some years ago Meves discovered that in the bee half the spermatocytes are very small and degenerate without forming functional spermatozoa, and Meves compared these to polar bodies, but seems not to have suspected their significance in relation to sex-production. Morgan discovered in *Phylloxera* and von Baehr independently in *Aphis saliceti,* that a similar degeneration of half the spermatocytes takes place, and further, that these are the ones that fail to receive the "accessory chromosome" (*i. e.,* the X-element). Functional spermatozoa are produced only from those spermatocytes into which the accessory chromosome passes, and these obviously correspond exactly to the female-producing class in the ordinary case. These observations have since been extended by Miss Stevens to a considerable number of species of aphids. A complete explanation is thus given of the fact, which has long been a puzzle, that in these animals all the fertilized eggs produce females. Not less interesting is the discovery by Morgan and von Baehr that in both the forms in question the males, though produced from the females strictly by parthenogenesis, have one chromosome fewer than the females. The male-producing egg must therefore eliminate one chromosome, and this, we can not doubt, is the X-element. What has hitherto seemed to be a stumbling-block in the way of the general conclusion is thus seen to be in reality a remarkable confirmation.

To what extent these conclusions, based upon the study of the arthropods, will be found to hold true for other organisms remains to be seen. The experimental results of Correns on the flowering plants, which harmonize completely with the cytological results on the insects, certainly seem to give good reason to expect that the general principle involved will be found to hold true of a large series of forms.

IV. SEXUAL PREDESTINATION AND HEREDITY

Deferring for the moment the question of the sex-ratios, let us now attack the most difficult but perhaps most interesting part of our inquiry, which concerns the nature of the sexual predestination and its relation to the phenomena of heredity in general.[7] In the air-breathing arthropods, as has been seen, a dual sexual predestination of the spermatozoa is clearly seen. Does such dual predestination exist also in case of the sexual eggs? Could we rely on the cytological evidence alone we should unhesitatingly say, no; for it is clear that all the mature eggs are cytologically alike. Moreover, in the aphids and daphnids and rotifers the sexual eggs are all alike destined to produce females; and although it is possible that a male-producing class degenerates (like the corresponding class of spermatozoa), there is no evidence of this. The facts here evidently suggest

[7] Here again caution in our use of terms is necessary. Obviously in the cases we have been considering the spermatozoa are, in a purely descriptive sense, predestined as male-producing and female-producing. But it by no means follows that they are predetermined as male and female or even that they are male-determining and female-determining. Sexual predetermination and sexual predestination must not be confused, as is clearly shown by Corren's discovery that the pollen grains of diecious flowering plants are prospectively predestined as male-producing and female-producing, though their immediate products (the rudimentary prothallia) are all males. It would seem that there are here two kinds of males, which give rise, respectively, to male-producing and to female-producing gametes. Clearly, the definitive determination of maleness or femaleness only occurs when all the factors necessary to their production have been brought together. This *may* be effected before fertilization ("progamic determination" of Haecker), but may also first ensue upon union of the gametes ("syngamic determination").

that the eggs are determined as females by their combination with the spermatozoa, and that fertilization may here be considered as the immediate determining cause of the female sex. In the bees and other social Hymenoptera this conclusion is still more probable, even though the Dzierzon theory fall short of a complete demonstration. But this does not yet touch the root of the matter. It is more than possible that even in organisms that are incapable of parthenogenesis the unfertilized egg may in itself bear a sexual "tendency" which would cause it to develop into a male or female could parthenogenesis take place. This is shown by the bees and ants where the unfertilized sexual eggs produce males, and the conclusion seems unavoidable that all bear the male tendency. Both here and in the rotifer (if Maupas's conclusion be correct) the innate tendency of the egg is male; but this is not a fixed predetermination since it is reversed or suppressed by fertilization.

V. MENDELIAN THEORIES OF SEX-HEREDITY

We are thus brought to the central problem of sex-production, namely, the nature of the sexual tendencies of the gametes and their interaction. Can sex be treated as a form of Mendelian heredity, in which the gametes bear male and female tendencies or factors that correspond to those which represent the dominant and recessive members of a pair of allelomorphs? Should we think of maleness and femaleness as due to the presence in the egg of specific male and female determinants that disjoin in maturation and recombine in fertilization? That sex may be such a phenomenon was first suggested by Strasburger, and the conception has since been more fully developed, first by Castle and afterwards by Correns and Bateson, each in his own way. There are many facts that seem to speak in its favor. Each sex seems to show indications of the presence of the opposite sex in a latent or recessive condition. In hermaphrodites both sexes are present in the active state and may either appear side by side or may dominate successively. In diecious forms there seems to be no escape in certain cases from the conclusion that opposite sexual tendencies disjoin in the maturation divisions. One of the best examples of this is given by the diecious mosses, already referred to. As the Marchals's work shows, each spore and all of its products is irreversibly predetermined as male-producing or female-producing, and spores of both kinds are found in the same capsule. It would seem, therefore, that the two tendencies must be brought together in fertilization; and we should expect to find that the zygote or its products (the sporogonium) should combine the two. Such is indeed the fact. Moss plants (gametophytes) formed by regeneration from the stalk or wall of the sporogonium are either actually hermaphrodite or produce hermaphrodites in a succeeding generation (again formed by regeneration)—a condition never found in the normal gametophytes developed from the spores. But since the spores, formed by the two maturation divisions from the mother cells in the sporogonium, are again strictly male-producing or female-producing, the sexual tendencies must be disjoined by these divisions. Translating this into cytological terms, cells that contain only a single or haploid series of chromosomes bear but one tendency, male or female; while those that contain the double or diploid series bear both tendencies. The same appears to be true in the liverworts (*Marchantia*) according to the observation of Noll and Blakeslee.

With this the facts in the aphids and similar cases, as far as they go, seem to be in essential agreement. The summer parthenogenetic eggs form but one polar

body, and, as shown by Miss Stevens and others, they undergo no reduction. All these eggs produce females; but the male tendency must be present in a latent or recessive form, since males are ultimately produced without fertilization. In the maturation of the male-producing egg but one polar body is formed and no general reduction occurs. But, as already stated, the males nevertheless contain one chromosome fewer than the females, and the male egg must, therefore, in some way eliminate one chromosome, *i. e.*, reduction occurs in the case of one chromosome-pair. It can hardly be doubted that this pair is formed by the two X-elements (accessory chromosomes). At first sight, therefore, the conclusion seems inevitable that one of the X-elements bears the female tendency, the other, the male. It is probable that a similar process occurs in the bee and the ant. In the latter cases the eggs must, of course, originally bear the female tendency; but after the formation of both polar bodies all bear the male tendency; and it seems again at first sight impossible to avoid the conclusion that the female tendency is eliminated in the course of maturation. The same conclusion is indicated by Maupas's results on *Hydatina*.

It is evident from these facts that the explanation of sex-production is to be sought in a mechanism that is essentially similar to that involved in alternative heredity, and that a strong case can be made out for the Mendelian interpretation on this basis. This interpretation has been worked out in three forms, which exhaust the *a priori* possibilities. These are, first, that both sexes are sex-hybrids or heterozygotes (Castle); second, that the male alone is a heterozygote, the female being a homozygote recessive (Correns); third, that the female is the heterozygote, the male being a homozygote recessive (Bateson). I will very briefly examine each of these hypotheses.

The earliest of the three was that of Castle, according to which the fertilization formulas would be

Egg ♀ + spermatozoon ♂ = zygote ♀(♂) (female)
Egg ♂ + spermatozoon ♀ = zygote ♂(♀) (male)

or

Egg ♀ + spermatozoon ♂ = zygote (♀)♂ (male)
Egg ♂ + spermatozoon ♀ = zygote (♂)♀ (female)

according as the dominant character is borne by the egg or the spermatozoon. In either case a selective fertilization must be assumed, since only gametes bearing opposite tendencies unite.

This interpretation encounters two principal difficulties. One is the necessity of assuming selective fertilization, which, though possible, seems *a priori* improbable.

The other is the case of the bee and some other hymenoptera, which was pointed out by Castle himself but is now seen to be even more serious than he supposed. In the bee all the eggs after forming both polar bodies produce males if unfertilized, females if fertilized. Under the hypothesis, therefore, the female tendency must be derived from the spermatozoon. But this is a *reductio ad absurdum;* for the male is derived from an unfertilized egg which has by the hypothesis eliminated the female tendency. Castle offered the very ingenious explanation, based on the results of Petrunkewitsch, that the testis is derived from the polar bodies, which contain the female tendency. But this exit from the difficulty seems to be closed by the work of Sylvestri on certain of the Chalcidæ (*Ageniaspis, Litomastix*) and that of Schleip on the ant (*Formica*), which clearly proves that the products of the polar bodies in these forms do not in fact enter into the composition of any part of the body, yet the sexual relations are the same as in the bee. This difficulty seems to me to constitute a formidable obstacle

not only to Castle's hypothesis, but to the whole Mendelian interpretation.

The second hypothesis is that of Correns, which assumes the male to be a sex-hybrid while the female is a homozygous recessive. The fertilization formulas are accordingly

Egg ♀ + spermatozoon ♀ = zygote ♀♀ (female)
Egg ♀ + spermatozoon ♂ = zygote (♀)♂ (male)

This conclusion is based on the following beautiful experiments. Crosses between monecious and diecious flowering plants show that the monecious character behaves like a "unit character" which is recessive to the diecious. If reciprocal crosses be made between the monecious *Bryonia alba* and the diecious *B. dioica* the results are as follows: Female *dioica* crossed with male *alba* gives all females. The reverse cross gives half males and half females. From the fact that all the offspring of female *dioica* × male *alba* are females Correns concludes that all the eggs bear this tendency, which dominates the monecious character of the male parent. In the reverse cross the diecious character again dominates, but in this case is derived from the male parent. The appearance of the two sexes in equal numbers must therefore mean that half the pollen grains bear a dominant male tendency and half a recessive female. A similar result is reached by Noll by experiments of a quite different character on the hemp, but the proof seems to me less cogent.

Correns's experiments are of admirable ingenuity and his results seem at first sight to be open to but one conclusion. His interpretation renders the hypothesis of selective fertilization unnecessary; for the chance fertilization of any egg by any spermatozoon explains the numerical equality of the sexes in the same way that it explains the equal numbers of the two classes of offspring of an ordinary Mendelian cross between a homozygote recessive and a heterozygote. An obvious difficulty at once appears, however, in the parthenogenetic forms; for here the parthenogenetic females must bear both tendencies, since they, sooner or later, produce males without fertilization. We need not enter into Correns's suggestions in regard to the aphids and phylloxerans, since they are contradicted by the facts of the spermatogenesis. In case of the bee, he adopts Beard's supposition that there are two kinds of eggs—sexual female-producing, which require fertilization, and parthenogenetic male-producing. In the latter the original female tendency is replaced by the activation or setting free of a male tendency previously latent.[8] A similar explanation might be applied to the aphid, phylloxeran or daphnid. But does not such manipulation of the sexual tendencies greatly weaken the force of the Mendelian interpretation? To me it seems that if the sexual tendencies may thus be shifted back and forth between the active and latent states, the interpretation loses most of its explanatory value.

Can we then explain the difficulty in question by reversing Correns's hypothesis, assuming the male to be the homozygote, the female the heterozygote? This is the hypothesis of Bateson, who further suggests that different species or groups may differ in respect to the sex that is homozygous. The fertilization formulas now become:

Egg ♀ + spermatozoon ♂ = zygote ♀(♂) (female)
Egg ♂ + spermatozoon ♂ = zygote ♂♂ (male)

But new and even more serious difficulties now arise. If the male be homozygous in the ordinary forms of insects, what

[8] To understand this it must be borne in mind that Correns regards each "active" sexual tendency (whether dominant or recessive) as accompanied by a "latent" (not to be confused with a recessive) opposite tendency. Such a latent male tendency in the female, upon becoming activated, would dominate the female.

sense can be found in the production of two forms of spermatozoa? Still worse is the dilemma presented by the parthenogenesis of the bee or ant. If we here assume that the egg eliminates the female tendency in maturation, fertilization should produce a homozygous male, which is contrary to fact. If, on the other hand, we assume the male tendency to be eliminated, parthenogenesis should produce females, which is also contrary to fact. The only escape from this seems to lie in the assumption that if unfertilized the egg eliminates the female tendency, if fertilized, the male.[9] But can we regard this as probable?

VI. A PROVISIONAL FORMULATION OF THE BASIS OF SEX-PRODUCTION IN ANIMALS

I think it must be admitted that until these and various other specific difficulties have been satisfactorily met the Mendelian interpretation will fall short of giving an intelligible or adequate explanation. The general evidence in its favor is so strong that we may perhaps hope to see these difficulties cleared away by further study. In the meantime it seems to me that we shall do well to hold as closely as possible to what we actually see of the basis of sex-production in the tracheates. What we see is that males are produced from zygotes that contain but a single X-element, females from those that contain two such elements. It is interesting to see how many of the difficulties of the Mendelian interpretation disappear under the assumption, naive though it may appear, that a single X-element in itself causes or determines the male tendency, while two such elements in association create, or at least set free, the female tendency. As far as the animals are concerned, must of the facts that have been reviewed, in respect to both fertilization and parthenogenesis, fall into line with such a view. Assuming its truth, the facts work out as follows. In ordinary sexual reproduction all the unfertilized eggs should after maturation bear the male tendency because one X-element is left in the egg after reduction. If capable of parthenogenesis with the reduced or haploid number of chromosomes, such eggs should produce males (as appears to be actually the case in the bees and ants). If fertilized by a spermatozoon that lacks the X-element, the egg still produces a male, for the same reason. If fertilized by a spermatozoon that contains this element, the egg produces a female because of the introduction, not of a dominant "female tendency," but of a second X-element. How this operates to produce a female we can hardly conjecture; but in order to give point to the conception, let us assume that the X-element contains factors (enzymes or hormones?) that are necessary for the production of both the male and the female characters; that these are so adjusted that in the presence of a single X-element the male character dominates, or is set free; and that the association of two such elements leads to a reaction which sets free the female character.[10]

[9] This suggestion is due to Professor Morgan.

[10] Many well-known facts indicate that each gamete may transmit both male and female characters to the offspring. So far as the eggs are concerned (and also those spermatozoa that contain the X-element) I am, therefore, of the opinion, expressed by Correns, Morgan and other writers, that every gamete contains factors capable of producing both the male and female characters, and that this is also true of all the zygotes. In a former discussion I suggested the possibility that the same activity that produces a male might, if reenforced or intensified, produce a female. A somewhat analogous quantitative interpretation of sex, based on the nucleo-plasmic relation, has been put forward by R. Hertwig. Such purely quantitative interpretations involve certain difficulties that are avoided by the formulation here suggested, which approaches more nearly to a Mendelian interpretation.

In what measure such a formulation of the facts may be adequate will find its test in the facts of parthenogenesis; and while these are not sufficiently known to give a positive result, they seem in the case of animals to be, on the whole, not out of harmony with it. We must clearly distinguish between parthenogenesis with and without reduction, for in the former case one X-element is eliminated, while in the latter case both are presumably still present. Parthenogenesis preceded by the formation of a single polar body without reduction occurs in the summer generations of aphids, phylloxerans, daphnids and rotifers, and in all of these females are produced, since the female chromosome-combination persists unaltered. The male-producing eggs likewise form but one polar body and do not undergo a general reduction. As already stated, however, in the aphid or phylloxeran they eliminate one chromosome (the X-element) and thus produce the male combination.

The crucial test of the assumption lies in the parthenogenesis of eggs which form both polar bodies; for if it be correct the egg which develops with the reduced or haploid number of chromosomes should produce a male, and that which develops with the diploid number a female.[11] The facts are not yet known with sufficient accuracy to admit of a decision, but with one or two possible exceptions the best known cases seem to be, on the whole, in harmony with this. In *Rhodites* the eggs are usually female-producing, and were long since described by Henking as undergoing a preliminary coupling of the chromosomes; but the diploid number is restored by a doubling of the chromosomes previous to cleavage. Henking interpreted both divisions as equational, and assumed that no qualitative reduction occurs. More recently Doncaster describes the female-producing eggs of the saw-fly *Pœcilosoma luteum* as also developing with the diploid number, in this case without a previous coupling and doubling. Both these cases are therefore in harmony with the assumption. In the ant and bee the male producing eggs were supposed by Henking (*Lasius*) and Petrunkewitsch (*Apis*) to undergo reduction followed by doubling, as in *Rhodites,* which would be a contradiction to the assumption; but neither of these conclusions is borne out by more recent work. Schleip's studies on the ant (*Formica*) leave little doubt that the unfertilized eggs of the workers develop, at least up to a late stage, with the reduced number (24) and that the fertilized female-producing eggs of the queen develop with twice this number. In case of the bee, likewise, the work of Meves on the spermatogenesis renders it almost certain that Petrunkewitsch was misled, the number 16, which he observed in the cleavage of the drone eggs, being the reduced number. The ant and bee therefore also fall into line with the assumption. A difficulty, on the other hand, appears in Doncaster's results on the parthenogenetic eggs of a saw-fly (*Nematus ribesii*), which is said to produce usually males, but sometimes females. Doncaster makes the extremely interesting observations that there are here two types of maturation, both polar bodies being formed in each case, but in one type reduction occurs, in the other it does not. If we could assume that the former type is male-producing, the latter female-producing, the general assumption would receive a strong confirmation; but the spermatogonia are described as dividing with the diploid number. If this is

[11] There is, however, a possibility that in female-producing eggs reduction might occur in respect to all the chromosomes except the X-pair, which would form the converse case to that observed by Morgan in Phylloxera.

correct, it seems to negative the assumption.

Although, therefore, many of the facts of animal parthenogenesis harmonize with the naïve assumption that the presence of one X-element means the male tendency, of two such elements the female tendency, we are not yet in a position to assert that this is always the case; and the problem may be complicated by the presence of factors still unknown. We are led to suspect that this is really the case by the apparent disjunction of the sexual tendencies that occurs in the formation of the asexual spores of plants. Botanical cytologists are agreed, I believe, that such spores develop with the reduced or haploid number of chromosomes, yet they may produce either males or females. This seems irreconcilable with the view that half the spores contain an X-element which is lacking in the other half. But we are led, nevertheless, to suspect from the facts known in animals that the male-producing spores may be characterized by the absence of some element that is present in the female-producing ones; and the detailed study of the chromosomes has given us so many cytological surprises in recent years that we may well await more intimate acquaintance with the facts in the plants before drawing any definite conclusion in this case.

I can only touch here upon the possible relation of hermaphroditism to the phenomena seen in diecious forms. If the hermaphrodite condition were a synthetic one, formed by the union of male and female tendencies that are separately borne as such by the gametes, a serious difficulty would be presented to the provisional formulation that has been suggested. But it seems clear from the experiments of Correns and others that hermaphroditism, at least in the higher plants, should not thus be conceived. Hybridization experiments seem to prove that the hermaphrodite tendency is borne as such by all the gametes, so that the heredity of hermaphroditism is closely similar to that of the spotted or "mosaic" type of coloration in animals. The hermaphrodite character is, in other words, a unit character which does not split into separate male and female tendencies in the gametes. There seems, accordingly, to be as much reason to postulate in this case a special "hermaphroditic factor" which liberates both sexual capacities, as a special mosaic or mottling factor in the case of mosaic pigmentation. I have no desire to spin hypotheses, but will suggest that the same general view as that suggested for the diecious forms can be applied to the hermaphrodite if we assume that all the gametes alike contain an X-element and in addition an "hermaphroditic factor" which enables both male and female characters to come to expression." It can, I think, be shown that the results of Correns's crosses can be interpreted in the terms of such an assumption; but it does not seem worth while to speculate in this direction until more is known of the facts.[12]

I wish very distinctly to say that in any case I should only regard the naïve formulation of the facts here outlined as a provisional one which may have no other value

[12] How little we yet know of the true nature of hermaphroditism is shown by the Marchals' results on the dicecious mosses. The hermaphrodites artificially produced by regeneration from the sporogonial tissue are in this case evidently synthetic, since they are formed by the union of separate male and female "tendencies"; but such hermaphroditism would seem to be of quite different nature from that of normally hermaphroditic species. The same experiments prove that there may likewise be two forms of males and females; for the apparently male or female plants produced by regeneration from the sporogonial tissue are potential hermaphrodites (as is proved by their regenerative offspring) and differ widely in this respect from the normal males and females.

than as a possible guide to inquiry. There are many reasons for suspecting that it does not reach the root of the matter. One of them is the failure to account for the significance of the Y-element, which is as characteristic of the male sex, when it is present, as is the double X-element of the female. Another is the possibility, which is perhaps a probability, that other factors than the chromosomes may play an essential rôle in sex-determination. The data do not yet allow us to draw a positive conclusion on many of the detailed questions of this kind. But our ignorance in regard to these more specific problems does not alter the fact that the cytological evidence has revealed a visible mechanical basis for the production of males and females in equal numbers and irrespective of external conditions; and this, I venture to think, constitutes a real and important advance in the investigation of the general problem of sex.

VII. THE SEX-RATIO IN RELATION TO THE CYTOLOGICAL BASIS OF SEX-PRODUCTION

We are thus led, finally, to the question of the sex-ratios as they appear in the light of the foregoing conclusions. It is well known that different species often exhibit characteristic differences in the ratio of males to females; and this fact has been urged by some writers as an argument against the existence of an intrinsic and uniform mechanism of sex-production and against the specific assumption that sex is transmitted as a Mendelian character. The cytological facts seem to me, on the contrary, to offer the most valuable suggestions for an understanding of the variations of the sex-ratio. This appears from a consideration of the extreme case where all the fertilized eggs produce the same sex, as in the aphids, daphnids and the like. A complete explanation of these cases seems to be given by the discovery that only the female-producing spermatozoa are functional. May we not here find a clue to the explanation of less extreme departures from the equal ratio shown in other forms? It is probable that the suppression of the male-producing spermatozoa in the aphids and phylloxerans was gradually brought about, and was connected by intermediate stages with the usual condition in which both classes of spermatozoa are equally functional. Stevens finds that in the aphids all degrees of inequality exist between the two classes of spermatocytes, though none of the male-producing class seem to give rise to spermatozoa. It seems reasonable to suppose that such a condition has followed one in which only a part of the male-producing class became impotent or degenerate. Owing to the enormous number of the spermatozoa, such a partial impotence of this class would produce no noticeable effect on the sex-ratio until it had proceeded very far. Sooner or later, however, the proportion of males from fertilized eggs would be reduced, and finally extinguished. Such a process would lead to the extinction of the species were it not for a compensatory parthenogenetic production of males, such as, of course, exists in cases where all the fertilized eggs produce females.

As bearing on this question I may recall the well-known fact that among the flowering plants a certain proportion of the pollen grains are often impotent, sometimes in a definite ratio. Correns, for example, finds that in *Mirabilis longiflora* there are three impotent to one functional; in *M. jalapa* the ratio is four to one. Such facts are most suggestive in their bearing on the whole question of sex-ratios, and the possibility of their alteration by external agents. Since the two classes of spermatozoa differ in nuclear constitution it is highly probable that they differ in respect to their meta-

bolic processes. It is, therefore, well within the range of possibility that the reaction between egg and spermatozoon may differ in respect to the two classes. Such physiological differences may vary in different species and may be capable of modification by external agents acting upon either sex. Again, the difference of mortality between the sexes, which is probably one of the modifying factors of the sex-ratio, may perhaps be traceable to differences of metabolism that have their original root in the sexual difference of nuclear constitution. In the directions here indicated lie many possibilities regarding the natural or artificial modifications of the typical sex-ratio of which no account has hitherto been taken. Until they have been thoroughly reckoned with, I think that all results upon the sex-ratios that are based upon general statistical and experimental inquiries must be taken with great caution. Taken as a whole, the evidence now indicates that in diecious organisms generally the basis of sex-production is primarily adapted for the production of males and females in equal numbers, and that departures from equality are due to secondary modifications.

VIII. CONCLUSION

A review of the ground that has been traversed will, I think, leave no doubt regarding the answer that should be given to the general question that formed our point of departure. The conclusion has become in a high degree probable that sex is controlled by factors internal to the germ-cells, that the male or female condition does not arise primarily as a response of the developing germ to corresponding external conditions. Such conditions may operate to modify the action of the internal mechanism, but the process of sex-production is fundamentally automatic. In so far as sex has been traced to a predetermination of the fertilized egg, or to a predestination of the gametes that unite to produce it, the problem of sex-production may be said to have reached a proximate solution. But it is perfectly obvious that this solution is proximate only, and has but opened the way to a more searching analysis of the nature of sex. Upon what conditions within the fertilized egg does the sexual differentiation depend? In some way, we may now be reasonably sure, upon the physiological reactions of nucleus and protoplasm; but the same may be said of any other form of heredity. The specific problem of sex here merges into the larger one of heredity and differentiation in general, and the minor problem acquires a broader interest through the hope that it gives us of attaining a solution of the major one. Into this aspect of the subject I will not now enter. I hope to have given some justification for the assertion, made at the outset, that substantial progress has been made in the exact analysis of the sex-problem. Recent researches have given good reason to believe that sex-production is governed by a common, and perhaps relatively simple principle. They have demonstrated that it has a definite morphological basis, which, even though its mode of action is not yet fully comprehended, is susceptible of accurate microscopical and experimental analysis. They have given a new point of view for the experimental and statistical analysis of the problem. And the progress already made encourages us to hope that a more complete solution may not be very far away.

The history of the subject throws an interesting light upon the methods of biological inquiry. The reform that is taking place in zoology through the extension of the experimental method has sometimes produced a disposition to exalt this method above others, and the same may be said in

respect to exact statistical research. Both these methods are indispensable. But it is well to remember that the sex problem was first attacked by such methods, and that they long gave inconclusive or wholly misleading results. The most fruitful suggestions for its solution were first given by morphological studies, in which minute cytological research has latterly played an important part, while the newer experimental work is bringing complete demonstration to these suggestions. It would be hard to find a better illustration of the futility of placing exclusive trust in any single method for the solution of any complex biological problem. If a definitive solution is to be attained it will be a result of the alliance between observation and experiment, between morphology and physiology, which is fortunately becoming the distinctive feature of modern zoology and botany.

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PROFESSOR ALFRED GIARD (1846–1908)

Science in France has suffered an untimely loss in the death of Professor Giard. He was stricken suddenly (d. August 8) while in the height of his activities, relatively young, keen in his interest in new biological tendencies. His influence had long been felt in the advancement of science; and his absence will be regretted not alone in his native country. He was one of the foremost naturalists of his day, a man of vast erudition, and of original views.

His bent for natural history showed itself from his earliest youth. As a child of six he was already a passionate observer of nature, helped and encouraged by his father, who found the time to scour with him the surrounding country, the streams, the woods, the moats of the fortifications of Valenciennes, his native town; in this way he began to lay up a store of valuable information by personal experience, and to acquire the veritable instruction and education which he himself recommends in an article, charming and profound, published a few days before his death.[1] As attentive in reading and assimilating the writings of his predecessors as in observing all that took place around him, he early acquired a ripeness of judgment and a knowledge of facts noticeable in his very first writings, and particularly striking in his thesis for the degree of doctor.[2]

Appointed professor of natural history in Lille in 1873, Alfred Giard rapidly organized a zoological center and trained many remarkable naturalists, among others Charles, Jules and Théodore Barrois, P. Hallez, P. Pelseneer, L. Dollo. His profound knowledge of botany, as well as zoology, enabled him to teach both subjects with equal success. An enthusiastic convert to transformism, he introduced this doctrine into France by his teachings and writings, in spite of the most active opposition.

In 1874 he founded at Wimereux, near Boulogne (Pas-de-Calais), a zoological marine station; it was a tiny building with but scanty accommodation for the numerous and busy workers who rapidly assembled there, but it was destined to accomplish much useful work, as will be seen by its output—the *Bulletin Scientifique de la France et de la Belgique*, has now its forty-second volume in press, and there are eight volumes in quarto of *Travaux de la Station Zoologique de Wimereux*. There he passed his holidays living among his pupils in the most informal way, exploring with them the shore at low tide, the sand-hills surrounding the laboratory, the woods and highways farther afield, amazing all by the extreme variety of his knowledge and his wide-spread erudition, and opening to their eager eyes many unsuspected biological associations. It is only to be deplored that Giard's results on the fauna and flora of the region of the Boulogne, studies which extended over a period of twenty-four years, remain unpublished. At the time of his death he was gathering together his voluminous

[1] "Education du Morphologiste," *Revue du Mois*, 10 Juillet, 1908.

[2] "Recherches sur les Ascidies composées ou Synascidies," *Archives de Zoologie Expérimentale*, t. I., 1872.