ent during the earlier stages of their existence, but that these differences disappear at the moment of fecundation. It has since been shown that the difference in staining reaction of the germ nuclei is probably of secondary significance only, but the view that a primary physiological difference between the germ-nuclei exists, is not necessarily excluded.

The question has arisen whether we are to deny the old biological conception of a sexually indifferent stage in the life history? It seems to me that this conception is as necessary and fundamental today as it ever appeared to be, and that we can not depart from it without involving ourselves in absolutely hopeless theoretical difficulties.

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Sex Determination in Relation to Fertilization and Parthenogenesis

It is not an easy task to attempt a brief discussion of the relation of sex determination to fertilization and parthenogenesis; for the fact may as well be admitted at the start that we are not yet in a position to make any general statement as to what that relation is, and it is my impression that the subject is not yet ripe for discussion. We are not yet, I think, in a position to conclude with certainty in any single case that fertilization can be considered as a sex-determining factor, not even in the classical case of the bee. Even in cases which at first sight seem clearly to show that fertilization is such a factor, consideration will show that we can not, or at any rate have not, shut out the possibility that fertilization may be determined by sex rather than the reverse. There is the same uncertainty regarding the relation of sex production to parthenogenesis. There is no constant relation between these two processes, for the parthenogenetic eggs of a single individual may in the same species produce females only, males only, or both males and females. Both fertilization and parthenogenesis, in fact, present us with a series of relations to sex production in which the common factor, if there be such a factor, still eludes us.

There are two primary data which, I think, must be taken as our point of departure in any attempt to discuss these problems. The first is the long-known fact that in a few cases, of which the best known are those of *Dinophilus apatris* and *Hydatina senta,* the eggs are visibly distinguishable by their size as males and females, before fertilization or even maturation. Neither fertilization nor maturation, accordingly, can here be a sex-determining factor. We only know, if the results of Maupas and Nussbaum on *Hydatina* and the more recent ones of von Malsen on *Dinophilus* be well founded, that in these cases the ratio between male eggs and female eggs may be modified by conditions of temperature, or nutrition, or both, that affect the mother before the eggs are laid; but the true interpretation of this is still very far from clear. The second primary datum is that in many insects, and probably in many other air-breathing arthropods, the spermatozoa are predestined in the constitution of their nuclei, as males and females, or better, male-producing and female-producing forms, in equal numbers. Here, however, our actual knowledge ends, so far as fertilization is concerned. We do not know in any single case whether the predestination exists in both eggs and spermatozoa in the same species. Until we can be sure on this point it is almost idle to speculate on the subject; for if such a double predestination exists there must obviously be a selective fertilization, such that each form of egg is fertilized by the appropriate form of spermatozoon; and if this be so, sex is not determined by fertilization, but fertilization by sex. Until this ques-

tion has been decided it will be hazardous to venture any conclusions as to the causal relation between sex and fertilization. We may, however, be quite certain that in parthenogenesis the egg alone is competent to determine sex; and for this reason one finds it difficult to avoid the feeling that this is likely to be true of eggs that are fertilized, even though we have direct evidence of this in only two or three cases. There is a certain amount of cytological evidence that such is actually the case, at least in the Hemiptera and Coleoptera, and probably in other forms that possess a pair of idiochromosomes or an odd chromosome. On the other hand, the strongest piece of evidence against this is, of course the long-standing one of the bee; yet even here one of several possibilities is that only those eggs are fertilized that are already predestined as females. This case, I believe, is not as yet closed.

For the foregoing reasons it seems to me that our best hope of a successful attack on the problem lies in the study of parthenogenesis; though we are here still confronted by too complicated and puzzling an array of facts to be at present surmounted by any one interpretation. The limitation of time forbids any adequate review of these facts, and I must limit myself to a single and, I fear, somewhat one-sided line of treatment. It seems to me that the most available stepping-stone towards the investigation of this problem is afforded by recently acquired evidence that sex production stands in some definite causal relation with the chromosomes and may be treated from the standpoint of the Mendelian phenomena, as interpreted by the Sutton-Boveri chromosome theory. It is certain that in many of the insects there is a particular pair of chromosomes that have a special and constant relation to sex production. There is perfectly clear evidence that the two members of this pair couple in synapsis and are disjoined in the reducing division. There is very strong, though indirect, evidence that one of them enters a male-producing spermatozoon, the other a female-producing one. A very definite material basis, therefore, exists for a treatment of the sex characters as if they were Mendelian alternates, sex determination, as opposed to sex heredity, being a matter of Mendelian dominance, more specifically of chromosome-dominance. I think that apart from the specific evidence in favor of this view a strong *a priori* argument in its favor is the approximate numerical equality of the sexes, which may be taken as the prevailing rule. The existence of a pair of chromosomes that are specifically related to sex production, and in respect to which the gametes of both sexes fall into two equal classes, gives a simple and natural basis for an equal production of males and females if we assume that these chromosomes embody respectively the male-producing and the female-producing factors. In other words, these two chromosomes may represent the hereditary bases of the male and female characters, respectively; and their relations to each other in respect to dominance may condition sex determination as opposed to sex heredity.

Let us briefly consider sex determination in parthenogenesis from this point of view. In the parthenogenetic egg sex might conceivably be determined either by elimination from the egg of the male or female element in maturation, or by conditions that affect the relations of dominance between the chromosomes. The hypothesis of elimination, which has been discussed especially by Castle and Doncaster, demands a reducing division, at least in case of the sex chromosomes; and such a division is not known to occur without at least a temporary reduction in the number of the chromosomes. This view may perhaps

give a true explanation in certain cases; but formidable, if not fatal, difficulties stand in the way of its acceptance as a general principle of interpretation. In the case of the bee, for example, as Castle himself pointed out, if it be assumed that the female element is uniformly eliminated in the maturation of the parthenogenetic egg, the female element must be reintroduced by the spermatozoon; but the spermatozoa are produced by males that arise from parthenogenetic eggs, which by the hypothesis have eliminated the female element. Castle ingeniously endeavors to meet this difficulty by taking refuge in the conclusion of Petrunkewitsch that the testes are not formed from the egg proper but from a fusion-nucleus formed by union of two polar nuclei, in which the female element is present; but until decisive evidence is available that the testes really have such an origin in the male bee it seems to me impossible to regard the explanation with anything but skepticism. But better and more direct evidence than this, free from any hypothetical element, is afforded by the observations on aphids, recently brought forward by Miss Stevens. If her conclusions are well founded, as they seem to be, in these animals no process of synapsis or reduction occurs in any of the parthenogenetic eggs, whether they produce males or females; though the sexual eggs and the spermatocytes undergo reduction in typical fashion. The principle of elimination here appears to be ruled out of court as a sex-determining factor, and it only seems possible to explain the result by the assumption that throughout the summer broods there is a uniform dominance of the female element, and that males are produced from eggs in which a reversal of dominance takes place. That something of the kind occurs is indicated by the fact that both in aphids and in daphnids the same parthenogenetic mother may produce both male and female offspring; and in the daphnids the condition in which this occurs is shown by the recent experiments of Issakowitsch to arise in response to a change of the environment.

Whether similar considerations of dominance and recessiveness will afford a general explanation remains quite an open question, but they seem at least sufficiently plausible to be taken as a convenient working hypothesis. By its aid we can work out on paper a formal explanation of the mechanism of sex production that will include nearly all known cases, and will also include the determination of sex by external conditions (if it be admitted that such a process takes place). It would not, I think, be profitable to go into such speculative constructions in detail here. They are but fireside dreams which may serve a useful purpose in the safe seclusion of the study, but really belong in the same *limbo* with the so-called 'fool experiments' which all of us at times secretly practise. I dare say the general view that I have briefly sketched will appear to some as only a restatement of the problem done over into the Mendelian jargon. I venture to think, however, that it is a little more than this. A real advance has been made if it has become possible to connect sex production with a definite nuclear mechanism that gives us a tangible handle by which to take hold of the problem. But I hardly need add that this should not be considered as giving more than a tentative point of attack. It is entirely possible that we are on a wrong track, that the so-called sex chromosomes are only associated in a definite way with the sexual characters, and have in themselves no causative influence on sex production. The whole chromosome theory of heredity, for that matter, stands unproved before the judgment seat. I repeat, therefore, that the subject is not yet ripe for discussion; and what we need now

is not more theory or discussion, but more observation and experiment. I believe that the chromosome theory as applied to the sex problem presents a sufficiently plausible face to be taken for a time as a guide to further examination of the facts. Perchance the true explanation may be found on the way, even should our working hypothesis prove a false leader.

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SEX-DETERMINING FACTORS IN PLANTS

IT is generally agreed that no true sex-determining factors for plants have as yet been recognized, and naturally a botanist would hardly choose the topic which has been assigned to me in this discussion. Claims are, however, constantly made that this or that environmental influence has been observed to modify slightly at least the percentage of the sexes in dicœcious plants. The extensive literature of such experiments and observations was summarized very fully and critically by Strasburger in 1900, and I need only allude to it here.

A great variety of factors have been tested both singly and in combination, but without positive results. Conditions of nutrition, as to both kind and amount, have been exhaustively studied and reports of success in influencing the sex ratio by this or that fertilizer are constantly made, and quite as constantly fail of confirmation. Laurent has recently (1903) claimed that an excess of nitrogen or lime favors the development of males in spinach, hemp, etc., while potash and phosphoric acid favor the development of females, but his results are not convincing.

Temperature, light and moisture conditions, relative age of parents, relative maturity of pollen, early and late planting, pruning, etc., have all been more or less elaborately tested without achieving results.

Gallardo (1901) reported that wild female plants of *Dioscorea* and *Clematis,* when transplanted into the botanic garden at La Plata, became hermaphrodite the next year, and the year following returned again to the female condition. The experiment was repeated the following year, with the same results, but it is hardly clear just what factor or factors were here concerned, and it is certain that transplanting generally has no such effects.

That the sex of seed plants can be changed by environmental conditions is, however, further shown beyond the possibility of question by the case of the anther smut (*Ustilago violacea*) which infects the campion (*Lychnis dioica* L.). Here the fungus, when present in the female plants, regularly leads to the development of stamens and the suppression of the pistil. The capacity to develop stamens must, in this case, be assumed to be present in the female plant, and the fungus is able to induce the conditions necessary to their formation and the suppression of the pistils, and thus provide for the development of its own spores. Elaborate experimental attempts by Strasburger to duplicate on uninfected plants the effects produced by the parasite led, however, to no results.

In the absence of positive data as to sex-determining factors in plants it may be well to note briefly some of the more conspicuous facts as to sex differentiation with which the student of reproduction and heredity in plants is confronted.

In plants at least sex-determining factors are to be sharply distinguished from factors which lead to sexual as contrasted with asexual reproduction. We must be careful, in discussing the factors which may determine sex, to distinguish two questions: first, as to the causes which lead to the occurrence of sexual cell fusion as con-