trol of sexual dimorphism is one of such moment that it might well be assigned to a special commission including both cytologists and experimental breeders. The subject of the physiology of ontogenesis, including experimental embryology, form regulation, and experimental morphology, is one in which American zoologists and botanists have made their country famous, yet the exploration of the subject has only been begun. The investigators should all come together from time to time to consider new lines of advance. As further examples of investigations needing cooperation I may mention the determination of biogeographic centers and the routes and means of dispersal; the basal instincts and reactions of organisms—but these will suffice as examples of subjects of common interest to all the biological societies; zoologists, botanists, bacteriologists, anatomists, physiologists, thermatologists and psychologists. Such subjects may not be left to the different societies separately. It is because none of the existing special societies can appropriately assume charge of these general biological topics that their interests have not been as much advanced as they ought to have been. Some attempt has been made to meet the need by occasionally arranging joint meetings between botanists and zoologists, and in the last two discussions of the naturalists a symposium has been held on some general biological topic. But it is clear that there should be a special society for the cultivation of these subjects.

The American Society of Naturalists was established in 1883 as an association of professional naturalists. The original call was signed by fourteen persons, all but one biologists. Although many geologists joined the society later, most of them subsequently withdrew to concentrate their interests on the Geological Society of America. Many other special societies have sprung from the loins of the Naturalists, but, for the most part, the individual biologists have clung loyally to the parent society. It has been suggested recently that the Society of Naturalists is an anachronism; that its interests are too diffuse; that we must concentrate now on the special societies; that, now her children are grown, the mother should die. With this view I do not agree. I have tried to show that there is not now less need but more of a synthesizing biological society with the following aims: To arrange for an annual discussion of some burning biological topic; to arrange with the special societies one session for technical papers of interest to both zoologists and botanists as well as biologists of other societies; to arrange, through the appointment of commissions from time to time, for cooperation in the control of biological nomenclature and for the cooperative study of certain large topics. Such commissions should be composed of those specially investigating those topics and should do what they can to encourage independent work also in these lines. They should report briefly each year to the society.

Next year the Society of Naturalists will celebrate the twenty-fifth anniversary of its birth. Can it do so more fittingly than by arranging a series of brief reviews of the progress in the past quarter of a century of the larger cooperative undertakings in biology, with suggestions as to their better organization?

C. B. Davenport

THE BIOLOGICAL SIGNIFICANCE AND CONTROL OF SEX[1]

THE NATURE AND SIGNIFICANCE OF SEXUAL DIFFERENTIATION IN PLANTS

You will pardon me if in discussing the subject which has been assigned I take my

[1] Five addresses given before the American Society of Naturalists at Columbia University, New York, December 28, 1906.

illustrations chiefly from the forms personally familiar to me. The researches of the past few years have demonstrated sexuality in the ascomycetes, the rusts and the yeasts, and some would see sexuality in slime molds and even in certain bacteria and blue-green algæ. At present one would hardly dare deny the possibility of sex in any group, however low in the scale of development. Processes so universally present among both plants and animals one would expect to have some significance in organic development and in the life of the individual. Yet very little is really known about the fundamental questions of sex. We do not know what constitutes a sexual process; what the real difference between male and female actually is; nor, finally, do we know what advantage, if any, the rather complicated sexual process has over other methods of reproduction. A mustering of the facts will enable one to say that apparently nothing is accomplished by sexuality that can not be equally well accomplished by purely non-sexual methods of reproduction.

The theory that the sexual union gives renewed vigor of growth would lead one to expect that forms that multiply exclusively by non-sexual methods would show signs of weakness and eventually die out. In fact, however, non-sexual forms are as vigorous as sexual ones. One could often wish that such were not the case when one finds cultures of sexual molds overcome in the struggle for existence by bacteria and non-sexual forms of *Penicillium*. It seems probable that a considerable number of forms among the flowering plants, of which the ubiquitous dandelion may serve as an example, have dispensed with the sexual method and reproduce parthenogenetically without signs of loss in vigor. Many examples could be given of higher plants which have been cultivated since historic times by non-sexual methods. During the last four years, the male and female races of a number of different species of the molds have been cultivated by means of non-sexual spores in separate test tubes where it is not possible for them to reproduce sexually. In two species 115 non-sexual generations have been reached without apparent change in vegetative or sexual vigor.

As to the variations which sexual reproduction is supposed to favor or to check by a blending of male and female characters, it can be shown by horticultural records that plants propagated by cuttings or by other non-sexual methods are less likely to vary than those grown from sexually formed seed. Yet distinct varieties do frequently arise non-sexually and are to be distinguished in no respect from varieties obtained from seed.

There is great difference of opinion as to what constitutes a sexual act. Nuclear union apparently takes place previous to formation of so-called apogamous embryos in certain ferns and would seem to take the place of the typical sexual process. If graft hybrids are possible, as seems probable from recent investigation, we have in this association of vegetative cells from two different individuals the blending of characters obtainable through the union of differentiated sexual cells. Nuclear fusions have been repeatedly observed in vegetative organs of higher plants. Moreover, by treatment with certain chemicals fusion nuclei may be obtained which divide with an increased number of chromosomes. When brought back to normal conditions the number is reduced to that usual to the plant. The phenomena have nothing to do with reproduction and may, therefore, be considered merely as a sacrilegious juggling on the part of the experimenter with the sacred x and $2x$—the gametophyte and

sporophyte—rather than as giving any evidence of sexual character. The experiments are interesting, however, in showing the extreme plasticity of the plant cell.

There seem to be a number of different stages in a sexual act which may be passed through more or less independently of one another. Cell union in many forms is not at once followed by nuclear fusion. In the Desmids, for example, the nuclei do not fuse till the germination of the zygospores and in the rusts a whole life cycle is interpolated between the sexual union of cells and the fusion of nuclei. The fact that in certain hybrids the maternal and paternal chromosomes seem to retain their individuality throughout the whole plant up to the reduction division in the formation of the sexual cells, would indicate that delayed fusion of chromatic substance may be a common phenomenon, although generally less easily detected than in the rusts.

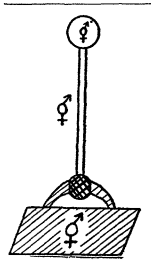
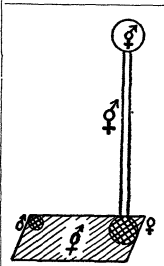
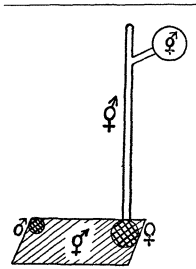
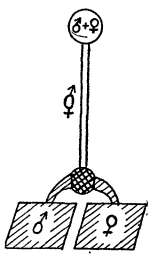
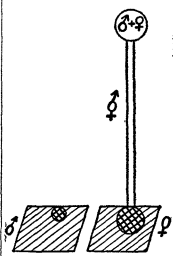
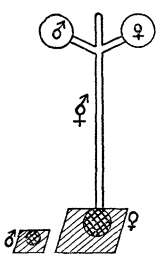
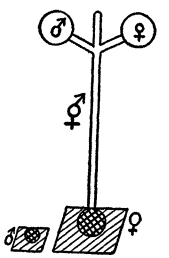
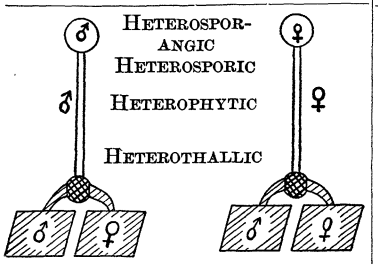
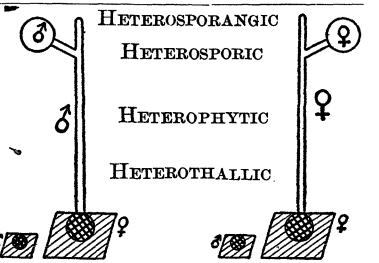
Not only may cell and nuclear unions occur independently of each other, but a distinct sexual reaction may take place leading to the formation and approximation of the sexual elements, though not to their union. In the mucors, when a sexual race of one species is grown between the male and female races of a different species, the sexual reaction between the races of opposite sex is shown by a white line due to the accumulation of imperfect hybrids. The reaction is sufficient only for the formation and mutual attraction of the conjugative branches. The second stage—the fusion of the sexual cells—occurs only when the opposite sexes belong to the same species and apparently can not take place between the opposite sexes of different species.

In treating the evolution of sex, it is customary to confine the attention to the progressive differentiation of the gametes alone. Differentiation of sex on separate individuals, whether or not accompanied by a differentiation in size of the gametes, would seem, however, to be the highest stage reached in the development of sex. The mucors may conveniently be taken as a basis of our discussion of this differentiation. There are comparatively few species in which the two sexes are united upon a single plant. If we assume this hermaphroditic group to be the more primitive, we have a progressive differentiation in two directions: first, to heterogamy, *i. e.*, to a constant dissimilarity in the gametes; secondly, to a constant dissimilarity in the sexual plants themselves. The large majority of the mucors have the sexes on separate individuals. Since the plants are capable of multiplication by non-sexual spores, a single sex may be indefinitely propagated non-sexually and the offspring thus obtained may be spoken of as male and female races.

It is difficult to conceive of a blending of characters in hermaphroditic species when the gametes may come from the same branch, even if they are in some species of different size. In dicœcious species zygospores have been obtained from matings of male and female races which in one species came from as diverse regions as China and Cambridge, Mass. In such forms the environmental conditions under which the sexually opposite races have grown may be sufficiently different to furnish a basis for the advantages assumed to accrue from a blending of maternal and paternal characters in the offspring.

The mucors form the only group of the lower cryptogams in which the presence of sexual races has been demonstrated.

In plants a differentiation is more or less apparent into a stage bearing the gametes and a stage bearing the spores. The accompanying figures represent diagrammatically the sexual character of these two stages in certain groups of plants. The stage

MUCORINEAE	BRYOPHYTES	PTERIDOPHYTES	PHANEROGAMS
SPORODINIA	FUNARIA	POLYPODIUM	
 HOMOSPORANGIC HOMOSPORIC HOMOPHYTIC HOMOTHALLIC	 HOMOSPORANGIC HOMOSPORIC HOMOPHYTIC HOMOTHALLIC	 HOMOSPORANGIC HOMOSPORIC HOMOPHYTIC HOMOTHALLIC	
PHYCOMYCES	MARCHANTIA	SELAGINELLA	LILIUM
 HOMOSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC	 HOMOSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC	 HETEROSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC	 HETEROSPORANGIC HETEROSPORIC HOMOPHYTIC HETEROTHALLIC
MUCOR MUCEDO			POPULUS
 HETEROSPORANGIC HETEROSPORIC HETEROPHYTIC HETEROTHALLIC			 HETEROSPORANGIC HETEROSPORIC HETEROPHYTIC HETEROTHALLIC

producing the gametes is the gametophyte. The stage arising from the germination of the zygote is the sporophyte. All forms which are hermaphroditic in the gametophyte are of necessity hermaphroditic also in the sporophyte. Every part of the mucor species *Sporodinia,* therefore (with perhaps exception of the sexual organs), contains both sexes. The same is true of some of the mosses and probably of all of the homosporous ferns. No representatives of this type exist among the flowering plants.

Phycomyces is dicœcious in its gametophyte. The zygospore formed by conjugation of branches from male and female individuals produces at germination but a single kind of germ tube which gives rise to a sporangium containing both male and female spores. The sporophyte therefore is hermaphroditic. That the germ tube in fact contains both male and female characters may be proven by forcing it to grow directly out to a vegetative mycelium before the formation of spores. The growth thus obtained is distinctly different from either the male or female individuals characteristic of this species and shows its possession of both sexes by the fact that it produces both male and female spores as well as sexually formed zygospores.

The liverwort *Marchantia* resembles the mucors in that its gametophyte is multiplied by non-sexual reproductive bodies and in that the sex of the spores of the sporophyte is not apparent until after their germination. I have been able to show that this liverwort corresponds to the *Phycomyces* type and its sporophyte must be considered hermaphroditic since both male and female spores are found in a single sporangium. As with *Phycomyces,* the determination of sex does not take place in the zygote but a sporophytic interval is interpolated between the zygote and the germ sporangium where the segregation of sex finally occurs. The heterosporous ferns illustrated by *Selaginella* differ from *Phycomyces* and *Marchantia* chiefly in the reduction in size of the gametophyte and in the fact that male and female spores are produced in separate sporangia. All four types discussed are dicœcious in gametophyte while hermaphroditic in sporophyte.

Mucor Mucedo has the sexes separated on different individuals as in *Phycomyces,* but two different kinds of germ tubes are formed by the germination of its zygospores. While some germ tubes are male and produce only male spores, others are female and produce only female spores in the germ sporangium. The sporophyte as well as the gametophyte therefore is unisexual. The same is true of the dicœcious flowering plants represented by the poplar. There are no ferns of this type and none are known among the mosses, but the sexual differentiation in the latter group has been but little investigated.

Forms like the bacteria apparently have not developed sexuality, others seem to have lost it. The loss may be permanent as in the habitually parthenogenetic forms, or merely temporary. Thus the sexual races of one of the mucors has been rendered temporarily neutral by cultivation for a few non-sexual generations at unfavorable temperatures and neutral races of several species have been found in nature.

It is among the algæ and fungi that the influence of external factors upon the method of reproduction has been most carefully investigated. The limits within which growth is possible are further apart than those within which the formation of the reproductive bodies can take place. Plants will grow under conditions where they can not reproduce. Similarly the conditions for the formation of sexual and non-sexual reproductive bodies do not always coincide, the limits being narrower

for the sexual than for the non-sexual spores. In many instances the influence of the external factors has been more or less definitely determined and by varying the cultural conditions one may obtain either form of fructification desired. Thus in the hermaphroditic mold, *Sporodinia*, one obtains exclusively non-sexual spores on a substratum deficient in nutrient but may obtain the zygospores by increasing the concentration of the nutrient.

Again, the conditions under which the male and those under which the female organs can form do not always coincide. We may illustrate this by the effect of the single factor light. The prothalli of homosporous ferns under minimum illumination may be brought to prolonged vegetative growth and thus the formation of both male and female organs be suppressed. When the amount of light is increased to a certain extent only male organs are produced from these sterile prothalli. To obtain female organs they must be exposed to a still greater illumination. Such suppression of the organs of a single sex on plants normally showing both sexes is not to be confused with sex determination in the offspring of dicœcious plants.

There are a number of facts which are assumed to indicate that in all dicœcious plants one sex is dominant and makes its appearance while the other remains latent. Thus a female plant is considered not pure female, but is supposed to contain the male character in a suppressed condition though not capable of being brought to light by simple changes in external conditions. Male and female willow plants are frequently found with flowers of the opposite sex, and as has been already explained, an hermaphroditic condition has been produced in *Phycomyces* which is normally dicœcious. Moreover, by cultivating this hermaphroditic growth by transfers of the vegetative mycelium, it eventually loses its hermaphroditic character and in a few mycelial generations is transformed into a male or female growth indistinguishable from one of the sexual races normal to this species. We know too little about what the fundamental differences between male and female actually are to be able to conjecture in what way this suppression or elimination of one sex is accomplished.

Especially interesting in this connection is the dicœcious plant *Lychnis dioica*. This wild pink, which has the sexes on separate individuals, is subject to the attacks of a smut fungus which is able to fruit only in the anthers or male organs. If it attacks a male plant it fruits in the male organs already present, coloring them violet. If a female plant is infected which normally never bears male organs, the growth of the parasite in some way stimulates its host to the production of male organs within which it may form its spores. This forms rather a striking example from the plant kingdom of doing good unto those that despitefully use you. Attempts have been made to artificially influence the sex in this plant, but entirely without success. It seems undoubted that in sporophytes of some plants the appearance of one sex can be suppressed in a similar fashion to that so well known for the prothalli of the homosporous ferns, but one is hardly warranted in assuming that in no forms the male and female individuals are ever sexually pure. The sex may perhaps be pure in the gametophyte while mixed in the sporophyte.

Some would question the sexual purity even of the gametes themselves. If the gametes contain but a single sex their development without conjugation in hermaphroditic forms should give rise to unisexual individuals—the male gamete to male and the female gamete to female individuals. Some experiments are in progress which it is hoped will throw some light

upon the sexual condition of the gametes in certain of the molds.

It is only by the further accumulation of facts in various groups of plants and animals that we may at length be in position to determine what if any unifying principle there may be in this wide-spread phenomenon of sexuality.

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The Biological Significance of Sexual Differentiation—A Zoological Point of View

The line of descent in multicellular animals is through a continuous or discontinuous series of sexual generations. In the latter case, there is alternation of generations, either of asexual and sexual or of parthenogenetic and sexual generations. So far as I know, the sexual generation is never absent in the first kind of alternation; there are, however, some parthenogenetic species in which males have never been found, though the structure of the females, or the natural history of the race, proves the former existence of males. There is only one feature common to all forms of sexual reproduction, and that is the union of ovum and spermatozoon to form a single cell, which has the capacity of developing into a new individual of the species. The biological significance of sex must, therefore, lie in the process of fertilization; and the interpretation of the fundamental significance of fertilization must be the answer to our problem.

Now fertilization is a more general phenomenon than sex itself, for it is characteristic of the Protozoa in the form of conjugation; and it appears to be a growing conviction among students of Protozoa that conjugation is universal in this group. Fertilization brings about biparental inheritance or amphimixis, and some have regarded this as its chief function, in view of the great importance of amphimixis for the process of evolution. But most zoologists regard amphimixis as a secondary function of fertilization, and find the chief significance of fertilization in the satisfaction of a periodic physiological need of the organism. The ovum usually requires fertilization as a stimulus to development; without it, in most animals, the processes of development either do not begin or soon cease. Observations on normal and artificial parthenogenesis demonstrate that it is not an indispensable requirement for development; however, in most parthenogenetic species fertilization-need arises in certain generations that alternate more or less regularly with the parthenogenetic ones; and those parthenogenetic species in which males are unknown have descended from sexual species, and moreover belong to specialized groups on one side of the main trend of evolution. Among Protozoa there seems to be a periodic need of fertilization to maintain the capacity of the species for reproduction.

We may then say, with the qualifications already indicated, that among animals at least the law of conjugation is as universal and imperative as the law of hunger. It is thus one of the most general of biological phenomena, with an element of obscurity in it that does not inhere in any other major problem of biology; for, as katabolism is combustion, the need of hunger to incite the individual to the taking of food is obvious; as the individual survives by adjustment to its environment, it must possess irritability and motility; but why the same food that satisfies for so long fails ultimately to support ebbing vitality among Protozoa, why the line of descent in Metazoa should pass through sexual generations —this is the mystery of physiology; and that salvation of the race should reside in