RECENT PROGRESS IN SOME FIELDS OF EXPERIMENTAL ZOOLOGY. I.

James Francis Abbott, Washington University

The two decades immediately following the publication of the "Origin of Species" were years of storm and stress both in biology and in theology. In the controversies of that period the two conceptions of *evolution* as contrasted with *special creation* on the one hand, and of the Darwin-Wallace explanation of the method of such an evolution on the other hand were inextricably confused. Accordingly, after the smoke of battle had cleared away and the hypothesis of evolution had found acceptance by the newer generation of working biologists, the tendency remained, to accept the Selection Hypothesis as unquestionably as the Evolutionary Hypothesis was finally accepted. Forgetting that Darwin's inductions were the result of long and patient accumulation of a mountain of data and that he himself had clearly recognized the difficulties and objections to many of his conclusions, it became the habit to "explain" all biological phenomena by this hypothesis and such *a priori* methods ran riot, particularly in the field of ecology. Theoretical biology in other words changed its attitude from an inductive to a deductive one and, as such, after a time, reached the limit of its resources, description replacing analysis in biological work.

Recently, however, the development of many new fields of biological inquiry and the increased application of biological data to the uses of the arts and medicine, together with the munificent endowment which biology has received both in Europe and America have greatly stimulated interest in the field and the inevitable reaction has set in. In the analysis of biological phenomena the genetic method has largely replaced the comparative method. Indeed the tendency of the present time is so largely analytical that "Experimental Zoology" is almost synonymous with "Modern Zoology."

As was to be expected, a similar examination of the method of Evolution was soon undertaken and the practical aspects of the study of Heredity, and Variation have, in addition, greatly stimulated inquiry in these fields. We now accept a Laboratory of Genetics or a Laboratory of Experimental Evolution as a matter of course, and it is perhaps not an overstatement that the great majority of investigators are concerned in some way or other with an analytical study of Variation or Heredity in some of its aspects.

The old demand of the anti-evolutionists to "show us a species that has unquestionably come into existence under the influence of natural selection" has not been silenced and the efforts of biologists to answer this demand, like the labors of the alchemists of old, while, indeed, so far they have not been exactly successful yet have been the source of a great many important discoveries or even the opening up of wholly new fields of research. Within the narrow limits of this review it will not be possible to do more than touch on a few of these results, nor will it be possible to cover the entire field.

The attack in general has been made in two directions: (1) The modification of Phylogeny or the experimental alteration of the specific type and (2) the modification of Ontogeny, in other words, analytical or experimental embryology.

Under the first head, experimental work is being done in selective breeding, germinal transplantation, and disturbance of the physiological balance of the organism in heredity. Under the second head may be ranged transplantation of tissues, effects of varied environments on developing eggs, hybridization and the determination or control of sex.

Pure Line and Pedigree Breeding

The botanists long since came to the conclusion that the limits of artificial selection are soon reached and that therein lies the most significant objection to the Darwinian hypothesis as originally outlined. The recognition of this fact accounts largely for the enthusiasm which greeted DeVries' so-called "Mutation Theory," since by the application of this hypothesis the production of new species by selection other than in a straight line, becomes possible.

The difficulties in the way of breeding animals in numbers have made the zoologists' contributions to this subject fewer and less conclusive than those of the botanists. The most important in recent times is the work of Tower with insects and Jennings and Woodruff with protozoa.

In a series of brilliant papers Jennings[1] describes the results of long continued and carefully planned breeding experiments with Paramecium. Since it is easily possible to get a generation or even two a day with this form, in the course of a year as many generations can be presented for study as might require 100 centuries for the human species to produce.*

Jennings finds that it is comparatively easy to produce structural or somatic alterations by environmental stimuli (changes of food, etc.). The environment is, of course, easily controlled. Such "acquired characters," however, are never reproduced in the progeny. The range of variation under the same conditions is great and it is possible by isolation of individuals to separate out many races. Each race has its own mean and range of variation,—its own "mode" in other words, but selection within this race is of no effect in altering the mean. Jennings insists that these races (which may differ either structurally or physiologically) are merely isolated by the experimenter, not created, and that they correspond in every way with the "pure lines" that Johannsen and other botanists have worked out in plants.

Herein is found an adequate explanation of regression, which has puzzled and obstructed the experimental selectionist so long. Suppose the goal aimed at is size. By selecting toward this character (in Paramecium *e. g.*) the smaller races or "pure lines" may be gradually dropped out until only one such remains and within that one, selection is of no avail in changing the average. Jennings states,—"In Paramecium, in the extensive study of many years for hundreds of generations, by exact statistical methods,—not one single instance was observed of variation in the sense of

1. Jennings H. S., Heredity, Variation and Evolution in Protozoa;—I. The fate of new structural characters in Paramecium with special reference to the question of the inheritance of acquired characters in Protozoa. *J. Exp. Zool.*—1908, 5, 577. II. Heredity of Size and Form in Paramecium, with studies of growth, environmental action and selection. *Proc. Amer. Philos. Soc.* 1909, 47, 393. "Heredity and Variation in the Simplest Organisms." *Amer. Nat.* 1909, 43, 321, (Popular resumé).

*Woodruff has kept continuous cultures of Paramecium under constant observation for over 2,000 generations.

an actual change in a race." Elise Hanel[2] finds practically the same conditions with respect to pure lines in so plastic form as Hydra, and it is getting to be more and more the belief of present day biologists that such pure lines are to be found in all species of animals and plants. How they arise and why they are so stable is the great problem of the future.

The Effect of Environment in Heredity

The issue between Darwinism and Lamarckianism was sharply drawn by Weissmann, who showed very clearly the distinction between soma (body cells) and germ plasm (reproductive cells). In America particularly, a great many biologists have an inclination, —suppressed or not—toward the Lamarckian position, which postulates the hereditary influence of environmental effects on the soma. This is the "Inheritance of Acquired Characters" which Weissmann denies *a priori* and which it has seemed impossible to demonstrate experimentally.

Many ingenious experiments have been tried to test the hypothesis. Heape[3] transplanted the fertilized egg of one variety of rabbit to the oviduct of a different variety and succeeded in producing uterine attachment and normal gestation. In every such case, however, the foster mother imparted none of her characteristics to the transferred offspring. Of course this result tells us nothing of what might take place if the transplantation were done *before* fertilization.

A great deal of work has been done in ovarian grafting in mammals. In general, such an experiment, if carefully performed, is successful, and the ovarian tissue lives in its new site. There is always the danger that in interpreting results, a regenerated ovary may be mistaken for the introduced tissue which has degenerated or been absorbed.

Guthrie[4] transferred the ovary of a black pure bred Leghorn pullet to a white pullet, replacing it with the ovary of the white

2. *Jenaische Zeitschrift.* 1907, 43, 321.

3. Heape W. Notes on the transplantation and growth of mammalian ova within a uterine foster mother. *Proc. Roy. Soc.* 1890, 48, 457; *l. c.* 1897, 62, 178.

4. Guthrie C. C. "Results of ovarian transplantation on body weight and egg weight in fowls." *Jour. Am. Med. Assoc.* 1908, 51, 1314; *ibid J. Exp. Zool.* 1908, 5, 563.

fowl. The birds began to lay six months afterward and the white one was mated with a black cock, the black one with a white cock. The controls, white × white, and black × black, gave uniform results consistent with their "pure" ancestry. The eggs from the pseudo-crosses gave, along with normal color, a number of variously spotted chicks which appeared to indicate that the residence of the introduced ovary in the foster mother's body had brought about a modification of the color pattern in the chicks, different from that normal to the race,—in other words, that the "soma" had influenced the "germ tissue."

Castle and Phillips[5] have criticised Guthrie's results[6] on the ground that the original ovary may have regenerated and Davenport[7] has recently repeated Guthrie's experiments and has negated his results. Castle and Phillips[5] have carried out similar experiments on guinea pigs and rabbits with negative results. Some of the most interesting experiments along this line have been carried out by Meisenheimer and will be referred to farther on.

In addition to such germinal transplantations, a variety of experiments in modifying the environment have been attempted to see if the operation of heredity can in such a way be controlled or altered.

Wesenberg-Lund[8] found that a seasonal dimorphism obtains in *Daphnia*,—the summer forms being smaller and with outgrowths on the body. Ostwald[9], however, has shown that varying the temperature at any season will produce these forms. On the other hand, Woltereck[10] claims that the temperature effect is indirect, that the nutrition is the effective agent and that there is a true seasonal dimorphism.

It is likely that the discordant results have been due to the fact that the various observers have dealt with different strains or "pure lines," some of which were predominant at some times,

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5. Castle W. E. and Phillips J. C. "On Germinal Transplantation in Vertebrates." *Carnegie Pub.* No. 144, 1911.
6. But see Guthrie, *Science* May 26, 1911.
7. Davenport C. B. *Proc. Coc. Exp. Biol. and Med.* 1910, 7, 168; *Jour. Morph.* 1911.
5. l. c.
8. *Biol. Zent.* 1900, 644.
9. Ostwald Wolfgang. "Exp. Unterruch. über die Saison. polymorphismus bei Daphniden. *Roux. Arch.* 1904, 415.
10. Woltereck R. *Verh. Deutsch. Zool. Gesell.* 1908, 234; l. c. 1909, 110.

and some at other times and that the environmental effect was illusory.

Kammerer[11] finds that by raising the temperature it is possible to make the males of the lizard, *Lacerta muralis,* (which is sexually dimorphic in color pattern) assume the female coloration,—a condition which is reproduced in the offspring.

The same experimenter[12] has worked with *Salamandra maculosa* which is sometimes viviparous, bringing forth larvae which have gills and behave as normal aquatic larvae, metamorphosing into land salamanders by atrophy of the gills. If, however, the mother be kept from water a small percentage of the young will be found to have already lost their gills when born. If, then, these mature they will give birth to gill-less young even if they themselves are not deprived of water.

Morgan[13] in a preliminary report on experiments now in progress described the results of breeding various races of Drosophila (the pomace fly) obtained by influencing the eggs or larvae with radium. Orange eyed, pink eyed, white eyed and short-winged flies thus produced,* interbred in various ways give very constant results in inheritance. These experiments will be referred to farther on.

An interesting experiment has been recorded by Sumner[14], in which growing mice were exposed to the outer winter temperature and compared with others bred in warmer rooms, with the result that the average tail length, foot length, ear, etc., was found to be considerably greater (as much as 30% in some cases) in the mice raised in the warm room. This effect seems to be transmitted to the second generation.

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11. Kammerer P. "Vererbung Erzwungener Farbveränderung," etc. *Roux. Arch.* 1910, 29, 456.

12. Kammerer P. Die Nachkommen der Spätgebornen *Salamandra maculosa* und der frühgebornen *S. atra. Roux. Arch.* 1907, 25.

13. Morgan T. H. Sex Limited Inheritance in Drosophila. *Science* 1910, 120.

*Since the mutants have appeared independently and since Loeb and Bancroft (*Science* 1911, 781) find that the radium effect is not specific or constant, Morgan himself is not certain that the radium is the real agent in producing the mutants.

14. Sumner F. B. "Reappearance in the offspring of artificially produced parental modifications," etc. *Am. Nat.* 1910, 44, 1; *l. c.* 1911, 45, 90; *Roux. Arch.* 1910, 30 (2), 317; *Jour. Exp. Zool.* 1909, 9.

In nearly all such work on the influence of environment on hereditary processes, the experiments have been carried on for too short a time and in many cases are too fragmentary or incomplete to enable one to draw definite conclusions or to be convinced that the new type is a permanent one. There is one brilliant exception. Tower[15] in two contributions has published the results of carefully planned and admirably executed experiments on the potato beetle which have been in progress for a decade and a half and are still being continued. It is fair to say that this work, in its thoroughness and completeness is one of the most important contributions to the analysis of the evolutionary process that has appeared in the past half century. It will be possible to allude to only a few of the results.

Tower has worked out in great detail the development and configuration of the color pattern of *Leptinotarsa* and decides that the localized stages of color pattern are "physiological and developmental and not phylogenetic." To quote his conclusion: In *Leptinotarsa* each species, as far as we can discover, starts in larval development endowed with a definite system of color-enzyme producing cells; that is, all start alike from a racial condition. Given this racial endowment, each species from the start modifies, holds in check, or increases the activities of the centers in its own manner, without any dependence upon the actions of its immediate parental or grandparental species. In the evolution of the color pattern, in the rise of new species, each species inherits this general racial system of coloration entire in its germ plasm, and the fundaments thereof appear in development. In the production of the new race, the capacity to modify this general color scheme is inherent in the germ plasm, and in heredity is transmitted to the offspring of the same kind as in the parent; but in the new race it is changed, the modified capacity producing new developments of the color centers which we recognize as the differentials of the new races or species."

Professor Tower then undertakes to modify artificially this color pattern by increasing the temperature, varying the humidity,

15. Tower W. L. "An investigation of Evolution in the genus Leptinotarsa." *Carnegie Pub.* No. 48, 1906. *Ibid. Biol. Bull.* 1910, 18, 285.

or the atmospheric pressure, etc. A *slight* increase or decrease in these environmental factors was sufficient to stimulate the activity of the color-producing enzymes, producing melanic or darker individuals; a *greater* increase or decrease of the factor inhibited them and produced albinic individuals. Tower thus showed that these environmental stimuli are not specific but general. These effects, however, are persistent in inheritance, so long as the stimulus is continued, and disappear immediately that stimulus is removed. There has seldom been so clear a demonstration of the impermanence of "acquired" or somatic modifications in inheritance.

Tower found, moreover, that the beetle does not mature all her eggs in one batch but in several batches, laid at successive intervals. It was thus possible to experiment on the insect by altering the environmental conditions during the maturation of some of the eggs and restoring them to the normal for others,—the control being thus the same individual. In this way a criterion of the specificity of the stimulus could be obtained. In some of these experiments mutations were the result of exposing the maturing ova to hot and dry conditions. In one case the change was a physiological one, *i. e.* a normally two-brooded form became five-brooded(!) a condition that persisted thirteen generations, until the cultures were destroyed by accident. In other cases various color-types were produced. These "mutations" like the five-brooded form were persistent in subsequent generations and when crossed with normal beetles the hybrids segregated in Mendelian ratio.

Another thing clearly established by Tower's work is the importance and universality of Selection in pruning away extreme variants and "limiting the reproductive population to the individuals nearest to the racial mean."

Developmental Mechanics

Many attempts have been made of late to analyze the factors of development and differentiation in the organism by interfering in some way or other with the normal course of development. A great deal of this work has been done by Prof. Loeb[16] during the

16. *vide* Loeb J, "*Dynamics of Living Matter,*" Macmillan 1906, and especially "*Die Chemische Entwicklungs-erregung des Tierischen Eies*" Berlin 1909.

past decade and a half. In spite of the brilliancy and daring originality of his work and of those of his school, the result has been not so much to really answer the questions for which an answer was sought as to stimulate further inquiry or even to open up wholly new fields for exploration and to reveal the intricacies and complexities of phenomena hitherto considered relatively simple. As the greater part of this work has been reviewed elsewhere in one way or another, only the most recent phases of it will be alluded to here.

Conklin[17] established the fact in the ascidian egg—and it was soon afterwards confirmed by others in echinoderm, molluscan, and other eggs,—that the protoplasm of the egg consists of different substances that can be distinguished by color. These "organ-forming substances" appear to be segregated and localized into different areas of the cleaving egg and to indicate a "preformation" of the egg antecedent to cleavage.

By the use of the centrifuge it has been found possible to shift the relative positions of these substances and thus further analyze their influence in development. Morgan and Lyon,[18] working with Arbacia, (a sea-urchin with a heavily pigmented egg), found that a rearrangement of the cytoplasmic constituents follows strong centrifuging, due to the different specific gravities of these substances; that the resultant stratification bears no relation to the egg axis and that while the cleavage conforms strictly to the induced stratifica-ion, gastrulation and subsequent differentiation is unaffected. "The factor that determines the median plane of the embryo is dynamic and not material." Morgan and Spooner[19] continuing the same line of work, have discovered that the micromeres of *Arbacia* arise in cleavage directly opposite the "micropyle," so called, or fertilization funnel, and cleavage is thus independent of the differentiated cytoplasmic substances. Gastrulation is also independent of them. Miss Spooner[20] also finds the same thing to be true of Cyclops. Getting at the problem in a different way, Morgan,[21]

17. *Jour. Acad. Nat. Sci. Phil.* 1905, 13; *Biol. Bull.* 1905, 8, 205.

18. Morgan T. H. and Lyon E. P. *Roux. Arch.* 1907, 24, 147. Also Lyon, l. c. 23, 151.

19. Morgan T. H. and Spooner G. B. "The Polarity of the Centrifugal Egg." *Roux. Arch.* 1909, 28, 104.

20. Spooner G. B. *J. Exp. Zool.* 1911, 23.

21. *Roux. Arch.* 1910, 29, 205.

Dederer[22] and Browne[23] have used pressure to disturb the relations of the blastomeres in eggs with "precocious specification" *i. e.* eggs with determinate or mosaic cleavage. By pressure the blastomeres may be shifted in their relative positions. In *Ciona* (a tunicate) and *Nereis* (an Annelid) such a procedure seems always to produce disturbances in the distribution of the localizing substances so that the larvae are abnormal. This appears not to be the case with *Cerebratulus,* a nemertine worm, (Dederer), nor *Cumingia,* a mollusc, (Browne).

Almost every imaginable chemical and physical alteration of the environment has been tried on developing eggs in the hope of discovering some specific effect, but although, as was to be expected, a wide range of abnormalities has been obtained, in only a few cases can it be said with certainty that a specific substance has produced a specific modification of the process of development. The famous lithium embryo of Herbst[24] is one such instance. In this case the Li. ion produces in the sea-urchin an "exogastrula" in which the gut is formed *outside* the pluteus larva. Recently another such specific effect has been obtained by Stockard[25] on the embryos of the Killifish (*Fundulus*). The action of the Mg. ion (chloride or nitrate) of a certain strength produces in the embryonic fish a fusion of the two eyes into a single cyclopean eye. In neither of these cases is there at present any reasonable connection between the cause and its effect. Such results are valuable in opening our eyes to the magnitude of the field that still must be conquered before we may enter upon a beginning of an understanding of the fundamental processes of development.

The specificity of the developing tissue with respect to its differentiation has been investigated by Harrison, Lewis and others in a series of brilliant papers, some of which antedate the limits of this review. By transplanting tissues or organs from one developing larva to another some most interesting results have been obtained. Lewis has shown[26] that any patch of ectoderm grafted over

22. l. c. 225.
23. l. c. 243.
24. Herbst C., *Mitt. Stat. Neap.* 1895, XI.
25. Stockard C. R. Artificial Production of a single median cyclopean eye in the fish embryo by means of Mg Cl_2. *Roux. Arch.* 1907, 33, 249.
26. *Am. Jour. Anat.* 1904, III; *Jour. Exp. Zool.* 1905, II.

the optic cup of a developing salamander larva will differentiate into a lens and conversely that an optic cup may be cut out and grafted into the tail or side of the body where it invaginates in due form and the contiguous ectoderm differentiates into a lens.

Transplantation of limbs and other parts of the mature organism has been accomplished in a great variety of forms by numerous observers. In general the capacity of an animal to endure this sort of treatment is a function of its degree of specialization or the specificity of its tissues and decreases as we ascend the animal scale. Much of this work has been done in connection with regeneration experiments. It is of interest to note, however, that by refined technique Guthrie and Carrel have accomplished limb-grafting in mammals and their success in taking out and replacing sections of blood vessels should offer wide possibilities for the surgeon. A section of the jugular vein of the cat *e. g.*, interchanged with a section of the carotid will function and become modified so that the characteristics of arterial wall are assumed by the vein tissue and vice versa. These experiments antedate the limits of this article and are familiar to most of its readers. Recently Pearl and Surface[27] have made end to end anastomoses of the oviducts of the fowl without interfering in any way with the functions of that organ.

Grafting offers a means of regenerative control, particularly of nervous tissues. Braus[28] has contended that nerve regeneration can take place in the absence of central or ganglionic influence in opposition to the view that regeneration of peripheral nerves cannot take place in the absence of the ganglion cell. Harrison[29] has repeated and extended Braus's experiments and by very careful and ingenious manipulation (involving the grafting together of an *aneurous* larva with a normal one which functions as a "nurse") has obtained results that lead him to the opposite conclusion, namely that there is no "auto-regeneration" or nerve development within a transplanted limb bud but that in every case a nerve branch (connected with a ganglion) grows into the limb bud and differen-

27. Pearl R. and Surface F. M. *Am. J. Phys.* 1908, 22, 357.
28. Braus H. "Einige Ergebnisse der Transplantation von Organanlagen bei Bombinator larven." *Verh. Anat. Gesell.* 1904, 18.
29. Harrison R. G. "Experiments in Transplanting Limbs." *J. Exp. Zool.* 1907, 7, 240.

tiates. It accommodates its configuration to the limb no matter what its source or original predestination. In a later paper, Harrison[30] continuing his former experiments on tadpoles, emphasizes his conclusion that the "ganglion cells are the dominant factor in the development of the nerve fiber; and that protoplasmic bridges do not play an essential role." An account of an interesting series of experiments has recently been published by Burrows[31], and Shorey[32] on the artificial culture of living tissues outside the body. In 1907 Harrison[33] published an account of his observation of the living developing nerve fiber of the frog removed from the body to a drop of lymph. The neuroblasts developed into nerve cells and fibrils and confirmed his view that such neuroblasts are always self-differentiating.

Burrows, working with embryonic chick tissues transferred to blood plasma (of chickens) confirms the observation of Harrison. He finds that other tissues than nerve tissue will grow with equal facility. The embryonic heart continues to beat normally for several days in such a medium. The differention, however, is strictly histogenetic and organs are not formed. Miss Shorey working with *Necturus,* along the same lines, comes to the conclusion that for such isolated cells or tissue elements to differentiate in artificial media, the metabolic products of other tissues must be present to act as differentiating stimuli. In other words her conclusion is the opposite to that of Harrison, i. e. that such primordia are self-differentiating. An inviting field for investigation thus opens to any one who can master the delicate technique required.

The Determination of Sex

For a long time the question of sex-determination,—of male as against female, and of sex-control,—of sexuality as against asexuality, (which is a different problem) has perplexed the mind of man, and many have been the fantastic hypotheses advanced

30. *Roux. Arch.* 1910, 30(2), 15.

31. Burrows M. T. "Growth of tissues of the chick embryo outside the animal body." *J. Exp. Zool.* 1911, 10, 63.

32. Shorey M. L. "Differentiation of Neuroblasts in artificial culture media." *l. c.* 1911, 10, 85.

33. *Proc. Soc. Exp. Biol. & Med.* IV, 140.

to cover the phenomena. Of recent years these theories have become more critical and precise and may be divided into two classes, (1) those which hold the sex-controlling element to be environmental,—particularly in connection with nutrition (the well known theories of Geddes and Thomson and of Schenk) and (2) those which hold that sex control is mechanical and intrinsic and independent of environment. The latter point of view has received strong support in the researches of the American school of cytologists whose results have been described in a recent review in this journal.* This point of view is not without its opponents at the present time. In particular Russo[34] opposes the current Mendelian interpretation of sex phenomena. Lecithin he finds to be a prominent constituent of germ cells and constitutes the *"mito-chondria"* and other "chromidial bodies" in the cell. By injection of lecithin Russo claims to have produced such structures, which he believes have an important bearing on the cell potentialities. To test this, he arranged a series of experiments with rabbits fed or injected with lecithin. He found that in such rabbits, the treatment markedly interfered with the "dominance" of certain color characters which usually follow the Mendelian ratio. Likewise he found that the feeding of lecithin caused its deposit in the gonad with the result that the ova thus stimulated gave rise almost exclusively to female offspring. Both these results run counter to the usually accepted idea of the mechanical sorting out of intrinsic "determinants" in the germ cell, whether these are embodied in the chromosomes or not. Russo's theory, indeed, leads back to the standpoint of Geddes and Thomson,—that sex is a matter of metabolism,—the female being anabolic, the male katabolic. Russo's work, in spite of its apparent exactness, needs confirmation, particularly in view of the precise results obtained by selective breeders, (in *Drosophila*, *Abraxis*, etc.).

In this connection it must be noted that Tennant[45] has discovered that in reciprocal crosses of two genera of sea-urchins, the

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*Guyer, p. 179.

34. Russo A. "Studien über die Bestimmung des weiblichen geschlects." Jena. 1909.

45Tennent D. H. The Domminance of Maternal or of Paternal characters in Echinoderm Hybrids" Roux. Arch 1909, 29, 1.

degree of predominance of maternal as against paternal characters is a function of the alkalinity of the sea water.

That food, or at least environment, is significant in the production of sexual individuals in parthenogenic strains has long been known in the Aphids and has been established in other animals by experiment. Shull[35] finds that, in the rotifer *Hydatina senta,* whereas starvation has the apparent effect of producing sexual individuals in parthenogenetic strains, the effect is rather qualitative than quantitative and must be ascribed to the presence of other chemical substances than food, such as ammonia compounds, creatin, urea, etc., in the culture medium. Shull believes, however, that internal factors are also involved in the production of sexual individuals, leaving it an open question as to whether alterations of these internal factors can be brought about by environmental stimuli (cf. Tower's work above). Whitney[36] and Nussbaum[37] have recently attacked the question of the production of sexual organs in *Hydra.* The former finds that starvation will not induce the formation of gonads in *Hydra* unless they are subjected also to low temperature, whereas an abundance of food following low temperatures suppresses the formation of testes and ova. Nussbaum claims that the temperature works only indirectly in affecting nutrition. On the basis of experiments conducted for many years he has claimed that an abundance of food favors egg formation, which again is practically the old claim of Geddes and Thomson. On the basis of many similar experiments it has been clearly demonstrated that environmental changes alter the cycle of parthenogenetic and sexual generations but it certainly remains unproven that they actually determine the sex.

A number of similar studies on other forms have recently been made, particularly with *Daphnia.* Woltereck[38] found not only that starving induced the production of sexual individuals but that superabundance of food produced the same result. McClendon[39] concludes on the basis of a variety of experiments with *Daphnia*

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35. Shull A. F. *Am. Nat.* 1910, 44, 146; *J. Exp. Zool.* 1910, 8, 311; *l. c.* 1911, 10, 117.
36. Whitney D. D. *Roux. Arch.* 1907, 24, 524.
37. Nussbaum M. *Pflügers Arch.* 1909, 130.
38. Woltereck *Verh. Deut. Zool. Gesel.* 1908, 234, and *l. c.* 1909, 110.
39. McClendon J. F. *Am. Nat.* 1910, 404.

pulex that "conditions which are adverse to the growth of the body cells, (viz. high temperatures, concentration of excretory products or disordered nutrition), either fail to retard the development of the germ cells [in such parthenogenetic forms] or overstimulate their development so that in either case the daphnid becomes sexually mature at a less developed stage."

Returning to the subject of sex-determination it is evident that those workers who have considered sex to be regulated by an internal automatic mechanism which is unaffected by environmental stimuli have a much more satisfying array of evidence to put forward. Quite apart from the question of the "sex-chromosome," if sex is treated as a character that segregates in some way in the gametes, in other words, that the individual is a sex-hybrid, the direct results of breeding experiments appear to harmonize with such an hypothesis in an astonishing way. Such results fall in line with the conception that sex behaves as do Mendelian "unit-characters," one sex being always heterozygous and the other homozygous. The best known work has been that of Doncaster and Raynor[40] on the moth *Abraxis grossulariata* and its (female) variant *lacticolor*. Crossing these types in various ways produces various divergent and complicated results, to record which would exceed the limits of space available for the present review, but although different hypotheses have been advanced to account for the facts it seems clear that only by treating the factors as Mendelian unit-characters can an intelligible interpretation be gained. Similar results have been obtained by Morgan[13] with the pomace fly, *Drosophila*. The red-eyed, white-eyed, pink-eyed and orange-eyed variants together with the short winged type produced as sports in the course of experimentation behave in crossing in every instance as Mendelian unit-characters, with the interesting addition that in most cases the character is "sex-limited" *i. e.* is carried by both sexes but becomes evident only in one and remains latent in the other,—a behavior similar to the heredity of color blindness in human beings.

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40. *Proc. Zool. Soc. Lond.* 1906, 125; *Nature* 1907, 76, 248.
13. Science 1910, 120.

The conception of the dioecious individual being a sex-hybrid receives strong confirmation of a direct nature in the ontogeny of a single individual where that individual suffers gradual castration. Geoffrey Smith[41] has made extensive studies at Naples of spider crabs parasitized by *Sacculina.* As in all crabs, the sexes are easily distinguished structurally. The parasitization effects a gradual castration of the host through an atrophy of the genital glands and ducts. Males thus infected by *Sacculina* showed every degree of modification toward the female type! The reverse is, however, not true of the females. It would seem, therefore, as if the male crab carries the potentialities of the sexual characters of both sexes, *i. e.* is "heterozygous," the male determinants being dominant over the female determinants or inhibiting them as one may prefer. Castration removes this inhibition, which would thus seem to be localized in the germinal tissue, and allows the female secondary sexual characters to appear. The mechanism of this change is not wholly clear. It has long been known, of course, that castration deprives the growing animal of some stimulus for the development of the secondary sexual characters and this has been referred to an internal secretion or "hormone." Cunningham[42] has formulated this into a general hypothesis. Smith contends that there must be several such "generative ferments," one of which stimulates the gonad to produce another or else is "worked up" by the latter into a controller of secondary sexual characters. That the mere extirpation of the gonad is not in itself sufficient to produce the result is evident from the work of Kellogg[43] who extirpated the gonad from the developing silk worm caterpillar without affecting the secondary sexual characters of the moth at all. Meisenheimer[44], moreover, has succeeded in transplanting the gonad from one sex to the other without producing any effect on the imago. In addition to transferring the gonads or castrating the caterpillars Meisenheimer also, at the same time, removed the rudiments of the wing in some individuals in order to see if the color pattern (which differs with the

41. Smith G. "Studies in the Experimental Analysis of Sex" I-II *Q. J. M. S.* 1909, 54, 577; III-IV *l. c.* 1910, 55.

42. Cunningham J. T. *Roux. Arch.* 1908, 26, 372.

43. Kellogg V. L. *J. Exp. Zool.* 1905, I, 601.

44. Meisenheimer E. *Verh. Deut. Zool. Gesel.* 1908, 84; also *ib.* "Experimentelle Studien zur Soma und Geschlechts differenzierung," I, Jena 1910.

sex) is dependent upon the presence of the sex cells. Wherever the wing-rudiment regenerated, the new wing was wholly uninfluenced by the change. He found, moreover, that extirpation of the sexual glands does not interfere in the slightest with the sexual instincts and reactions of the male moths.