SCIENCE

VOL. LXXI FRIDAY, FEBRUARY 21, 1930 No. 1834

SCIENCE: A Weekly Journal devoted to the Advancement of Science, edited by J. MCKEEN CATTELL and published every Friday by

THE SCIENCE PRESS
New York City: Grand Central Terminal
Lancaster, Pa. Garrison, N. Y.

Annual Subscription, $6.00 Single Copies, 15 Cts.

SCIENCE is the official organ of the American Association for the Advancement of Science. Information regarding membership in the Association may be secured from the office of the permanent secretary, in the Smithsonian Institution Building, Washington, D. C.

INHERITANCE IN A HEPATIC[1]

By Professor CHARLES E. ALLEN

UNIVERSITY OF WISCONSIN

I

THE studies here outlined were suggested by the presence in Sphaerocarpos of these advantageous conditions: (1) The presumable relative simplicity of inheritance in a haploid generation, yielding hybrid ratios that may be tested in comparatively small families, free from complications of dominance and recessiveness. (2) The opportunity for an exhaustive study of a given genotype, expressed through a clone ordinarily requiring little space but potentially unlimited in extent and duration. (3) The permanent adherence, in most species and races, of the four spores derived from each mother cell, making possible a virtually immediate determination of the genetic effects of meiosis.

While the predominant generation of Sphaerocarpos is simpler, because haploid, than the diploid organisms chiefly studied by geneticists, the phenomena of inheritance in this genus need not be expected, and do not appear, to be simpler in any other sense. The genus is probably the present climax of as long an evolutionary development as is the pea or the banana-fly. Sexual differentiation, so far as concerns gametes and the organs in which they are borne, is at approximately the highest point reached by any plant. Dioecism and sexual dimorphism are fixed and constant. The chromosome complex is comparable with that of any "higher" organism. Allosomes, in differentiation and in the correlation between their distribution and the appearance of sexual characters, resemble those of many Metazoa. The frequency of mutation is comparable with that elsewhere observed. In the longest series of experiments yet summarized,

---

[1] Address of the retiring vice-president of Section G—Botany, American Association for the Advancement of Science, Des Moines, Iowa, December 31, 1929.

1,273 gametophytes of known ancestry were determined as to sex and vegetative character. Of these, five—about 0.4 per cent.—were apparent mutants. Two were marked variants never before seen.

II

It is possible in plants of various orders to study the characters of gametophytes developed from spores recognizably derived from the same mother cell. Long ago Strasburger pointed out the possibilities offered by Elodea, whose pollen grains remain adherent in tetrads. An analysis of this nature has been made by Wettstein of the distribution of certain characters in moss hybrids, and a considerable number of studies of Basidiomycetes have dealt with what is in effect the intra-tetrad distribution of factors affecting syngamy.

In the course of the work with *Sphaerocarpos Donnellii* Aust., extensive attempts have been made to apply this method of intra-tetrad analysis. The far-from-simple behavior of certain characters later mentioned has interfered with the success of many of these attempts. Rather satisfactory results have accrued, however, with respect to the distribution of sexual, and of at least one pair of what may be called vegetative, characters.

Thus far each clone, however long under cultivation or to whatever conditions subjected, has remained strictly male or strictly female. My observations, and those reported by others, have disclosed no change in sexual expression, no suggestion of hermaphroditism or of intersexuality. The female gametophyte is now well known to possess a large X-chromosome; the male has a very small Y-chromosome; the other seven chromosomes apparently correspond in size in the two sexes. The X- and Y-chromosomes are separated in meiosis; two spores of a tetrad receive each an X-chromosome and develop, if they germinate, into female gametophytes; two receive each a Y-chromosome and develop, if they germinate, into male gametophytes. To this rule my experiments have afforded no exception.

Polyclady, fully described elsewhere, affects the structure of practically all gametophytic organs, conspicuously of the antheridial and archegonial involucres. Female polycladous plants are completely sterile. Polycladous males are fertile with nonpolycladous females. From every such mating that yielded more than two f_1 offspring, the progeny of each sex included polycladous and nonpolycladous clones. No exception, save one mutant, has been observed to the rule that, of the spores of any tetrad resulting from a mating of a nonpolycladous female and a polycladous male, two are genetically polycladous and two nonpolycladous. Thus, a character-complex affecting the whole plant, far transcending generic lines as these are understood among bryophytes, behaves in a strictly unitary fashion.

If the two character-pairs concerned in such a mating—namely, maleness-femaleness and polyclady-nonpolyclady—were inherited independently, the f_1 generation would consist of equal numbers of clones of four types: female nonpolycladous, female polycladous, male nonpolycladous and male polycladous. That these types do not appear in approximately equal numbers was early apparent. It is now possible at least partially to explain these deviations from a simple expectation.

The genetic constitution of all the spores of a tetrad is established if all, by germination, give rise to clones that live long enough for their characters to be determined. If three spores thus produce clones, then, on the assumption justified by experience that two are genetically female and two male, two nonpolycladous and two polycladous, the genotype of the ungerminated spores is established. If two spores germinate, and the resultant clones are alike either in sex or in vegetative character, on the same assumption the genotypes of the two ungerminated spores are known. Of thirteen f_1 families whose fathers were polycladous, seven, as shown in Table I, have yielded material for an analysis in terms of tetrads. In the table only those tetrads are included which, as just indicated, were decisive.

TABLE I

Genetic Types of Spore Tetrads (Decisive Cases Only) Among Offspring of Nonpolycladous × Polycladous

(p. = polycladous; np. = nonpolycladous)

Mating	I	II	III	Totals
	♀ 2np., ♂ 2p.	♀ 2p., ♂ 2np.	♀ 1np., 1p. ♂ 1np., 1p.	
14	—	1	—	1
28	2	1	—	3
29	5	2	1	8
31	12	7	3	22
32	13	6	5	24
33	7	1	2	10
40	—	1	1	2
Totals	39	19	12	70

Three classes of tetrads appear. Classes I and II are "two-type" tetrads; that is, both spores transmitting the same sexual tendency carry also the basis of the same vegetative character. Class III is composed of "four-type" tetrads, the spores of each representing the four possible combinations of sexual and vegetative characters.

The two classes of two-type tetrads differ in frequency of occurrence. Those of class I are about twice as numerous as those of class II, and a like difference holds for each family of any considerable size. The more numerous class is that whose spores represent the character-combinations of the respective parents; the smaller class, that whose spores represent new combinations of characters. A linkage between sex and polyclady is clearly indicated.

The familiar conception of sex-linkage is that of a character whose differential factor is borne on a sex chromosome. To apply that conception here, it would be necessary to assume a factor-pair borne on the X- and Y-chromosomes, and a crossing over during meiosis in about one third of the spore mother cells between each of the factors in question and some sex-determining factor. Apart from the questionable legitimacy of postulating a single pair of effective sex-determining factors (or even of factor-complexes behaving as units), the great difference in size between the X- and the Y-chromosome makes it extremely difficult to imagine a conventional crossing over between them.

A more probable explanation of the present facts seems to be that two chromosome pairs are concerned; one the X-Y pair affecting sex, the other a pair carrying the genetic bases for polyclady and its absence. The two chromosomes, one of either pair, derived from each parent must then tend to remain together and to pass to the same pole in each reduction division; and this tendency must be so strong that the chromosomes from the same parent do thus remain together twice as often as they are separated. Evidence is available in several angiosperms of an end-to-end attachment of chromosomes during meiosis which may lead to exactly such a behavior of chromosomes from the same parent as is here postulated. Such attachments are best known in Oenothera, but are not peculiar to that genus.

The occurrence of a minority of four-type tetrads bears directly upon the nature of meiosis. Cytological studies indicate that, in general, it is in the first reduction (heterotypic) division that the chromosomes of each pair are separated—one of the pair being in origin maternal, the other paternal. Evidence from plants is virtually unanimous on this point. In some insects, however, certain chromosome pairs, the sex chromosomes or others, are or may be separated in the second (homoeotypic) division. Now, if segregation occurs exclusively in the first division, the four nuclei ultimately formed (spore nuclei in the present case) must be, genetically, of but two sorts. That four-type tetrads occur implies that some segregation, of whole chromosomes or of chromosome parts, takes place in the second division.

Is it possible that in Sphaerocarpos *all* segregation occurs in the second division? A scheme for such segregation can be devised that will account for the production of two-type and four-type tetrads in the proportions here observed. But such a scheme involves rather far-fetched assumptions. On the simplest postulate of chance segregation in the second division only, equal numbers of two-type and of four-type tetrads should appear. *A priori* considerations then make segregation exclusively in the second division improbable. The argument is supported by the cytological evidence that segregation *appears* in virtually all plants studied to occur in the first division, and is made conclusive by the fact that in Sphaerocarpos the X-Y pair has been shown to separate in the first division—although the limited observations do not exclude the possibility of an occasional postponement of this separation to the second division.

It follows that some segregation is possible in the course of *both* divisions. Interestingly, a similar conclusion is reached by Dodge in his study of inheritance through ascospores in *Neurospora sitophila*. In that, as in the present case, two possibilities suggest themselves: either that some or most of the chromosome pairs are separated in the first division, at least one pair, however, separating regularly or occasionally in the second; or that all pairs separate in the first division, their separation being preceded by a crossing over in at least one pair of autosomes in the "four-strand" stage.

From the proportions shown by Table I for the respective classes of tetrads, it is easy to calculate the proportion in which clones of the four possible types would be expected to appear in the f_1 generation. The calculation gives: 9 ♀ nonpolycladous: 5 ♀ polycladous: 5 ♂ nonpolycladous: 9 ♂ polycladous. With this ratio may be compared the total numbers of clones of the various types obtained in f_1 progenies, as shown in Table II. Since knowledge of tetrad relationships is not essential here, this table includes much more material than did Table I.

The numbers of female types shown in Table II agree closely with the calculated proportions (266:148). The numbers for males depart rather widely from calculation, which, based upon numbers of males only, would give 118:213. As to this discrepancy, it is to be said that, since males succumb to unfavorable conditions more quickly than females, the major portion of the clones that died before their character could be satisfactorily determined were doubtless male. The females therefore present a more accurate picture of the genetic make-up of the population. Apparently it is necessary to assume in addition some difference in viability between the two types of genetically male spores.

TABLE II

RESULTS OF MATINGS OF NONPOLYCLADOUS × POLYCLADOUS; TOTAL OFFSPRING

p. = polycladous; np. = nonpolycladous)

Mating	♀ np.	♀ p.	♂ np.	♂ p.	p. (sex?)	Undet.
12	—	—	1	—	—	—
13	46	28	28	21	3	11
14	17	9	9	7	—	11
15	34	30	29	13	3	28
27	19	14	14	12	—	4
28	6	6	6	4	—	—
29	5	5	9	8	—	2
30	—	—	—	2	—	—
31	31	11	22	20	—	3
32	39	24	23	25	—	12
33	22	2	8	12	5	9
34	34	20	23	33	—	3
40	6	6	1	1	—	1
Totals	259	155	173	158	11	84

If another character-pair were concerned, ratios would evidently become more complex. Some matings have involved "tuftedness" in addition to sex and polyclady. The tufted character, as will appear, is variable, and results obtained with it must be stated cautiously. An additional difficulty is introduced by the fact that polyclady masks tuftedness, so that a polycladous tufted clone can not be distinguished by its appearance from a polycladous nontufted clone of the same sex. However, a few reasonably definite results may be cited. If a mating is made in which the father is polycladous and either father or mother is genetically tufted, then, apart from certain apparently possible but rare distributions of the tufted character, four classes of two-type tetrads and eight classes of four-type tetrads may be expected. A limited number of such matings have apparently yielded all the expected two-type classes and at least four of the eight expected four-type classes. Since the numbers of classifiable tetrads are yet low, and since the four-type classes must appear in but small proportions, it is probable that a mating of the sort in question would, in a numerous progeny, yield all the expected tetrad classes. Of those classes that have appeared, the small numbers do not justify a conclusion as to proportions, save that, as before, the two-type classes whose spores carry the parental combinations of genetic bases for polyclady or its reverse and sex are larger than those whose spores carry new combinations of these bases.

The results here given suffice to indicate that the intra-tetrad analysis of characters furnishes a direct method of attack upon the phenomena of Mendelian segregation, making possible, for example, a more accurate explanation than otherwise of crossing-over ratios; and also that it throws some light upon details of chromosome behavior that still elude cytological observation.

III

In consequence of the great difference in size between X- and Y-chromosomes, the female gametophyte of Sphaerocarpos possesses, cell for cell, a greater volume of chromosome substance than does the male. The advantage of the female in this respect is conservatively estimated at 50 per cent. Since the mother contributes a so much greater bulk of hereditary substance to the sporophytic progeny, it might be expected *a priori* that the constitution of a sporophyte would betray more evidence of maternal than of paternal influence.

An instance of preponderant maternal influence in the sporophyte appears in the inheritance of the tendency for spores to adhere, or not to adhere, as the case may be, permanently in tetrads. All the spores produced by any sporophyte are adherent or separate according as the mother of that sporophyte carried the one tendency or the other, and quite independently of the genetic constitution of the father. The tendency in question is sex-linked in transmission, although it appears in an asexual generation. Its inheritance has been tentatively explained by a factor carried on the X-chromosome and hence transmitted only through females.

A behavior perhaps closely comparable is observed in certain interspecific hybrids. Most attempts at crossing *S. Donnellii* and *S. texanus* Aust. have failed. But numerous hybrid sporophytes have been obtained from female plants of a strain of *S. texanus* from Arkansas mated with male plants of *S. Donnellii,* and a very few from a similar cross involving plants of *S. texanus* from Mississippi. The reciprocal cross has not yet succeeded. The most readily recognized distinctions between the two species are in the form and sculpturing of the spore and tetrad walls. In these respects all the spores and tetrads produced by the hybrid sporophytes resemble those of the maternal species. Such spores have thus far refused to germinate; but so far as the results go, the inheritance of spore-form and -structure follows the same rule as does that of spore-adherence or -separation. It may or may not be of wider significance that the only sporophytic characters whose inheritance it has yet been possible to study are determined by the genetic constitution of the mother.

The possible transmission of a preponderant maternal influence through the sporophyte to f_1 gametophytes is a less simple matter. The X-chromosome passes, apparently intact, to the female gametophytes; the Y-chromosome to the male gametophytes. With respect to the autosomes, the female and male gametophytes are apparently alike; apart, therefore, from differences between the sexes correlated with the presence of an X- or a Y-chromosome, no preponderant influence, either maternal or paternal, would be looked for in the f_1 gametophytes. Nevertheless, with respect to two characters something like a predominant maternal influence seems to be demonstrated in this generation.

One character is that designated "semisterile." Several semisterile male clones originated in plants of a single group, probably of common origin. They produce few antheridia. The semisterile character has remained constant through vegetative multiplication for more than eight years. A semisterile male mated with a tufted female produces typical and tufted offspring of both sexes, the typical (nontufted) tendency in this case being apparently inherited from the semisterile male ancestor. But no semisterile male, mated with a typical, tufted or appendiculate female, has ever produced semisterile offspring. The obvious explanation, that spores are formed carrying the semisterile tendency but unable to germinate, seems to be negatived by the fact that in numerous cases three, and in fewer instances all four, spores of a tetrad have germinated. It appears thus far, then, that the semisterile tendency, though constant so far as vegetative multiplication is concerned, can not be transmitted by a male parent through gametes and spores.

The second character, "cupulate," appeared in a male mutant. A cupulate male bears small crowded antheridia subtended by involucres which are predominantly saucer- or cup-shaped. This character has remained constant for five years through vegetative multiplication. The clone has proved fertile in two matings. In the one f_1 family obtained, no cupulate offspring appeared. So far as present results show, the cupulate tendency also is not inherited from the male parent through gametes and spores.

Thus phenomena suggesting the exercise of a predominant effect by maternal substances are found in both sporophyte and gametophyte. Those observed in the sporophyte may be explained by influences emanating from the X-chromosome; those noted in the gametophyte are not thus readily explainable, unless it can be imagined that factors borne on the X-chromosome may, by crossing over or by other means, be transferred to male progeny.

However, such a failure of paternal characters to reappear in f_1 gametophytes has much in common with certain instances of matrocliny in angiosperms which now tend to be explained in terms of cytoplasmic inheritance. A similar conception is nowhere more applicable than in a bryophyte, the cytoplasm of whose zygote is almost exclusively maternal.

IV

A somewhat similar failure of paternal tendencies to manifest themselves in the offspring may assist in explaining the puzzling nature of the inheritance of "tuftedness." This character distinguishes certain clones of *S. Donnellii,* the frequency of whose appearance in my original cultures suggests that tufted races are not uncommon in nature.

Tufted clones of either sex are marked by peculiarities in manner of growth and to some extent in vegetative structure, but most conspicuously by aberrancies in the forms of archegonial and antheridial involucres. A tufted clone produces tufted, typical and transitional branches, each of which may become an independent plant. The appearance of such a variety of branches is comparable with the variation that occurs among the branches of a variegated clone of Coleus, or with the less frequent appearance of bud sports in Citrus. In Sphaerocarpos the sporting process is reversible; a clone originating in a tufted branch gives rise sooner or later to typical branches, and a strictly typical branch from a tufted clone produces a clone that in time includes tufted branches. On the other hand, strictly typical *clones* exist which never produce tufted branches. Tufted clones and typical clones, then, differ genetically.

Their genetic difference is shown in another way. The f_1 progeny of a mating between a typical and a tufted clone includes both typical and tufted gametophytes of each sex. A mating between two typical clones gives rise to a gametophytic progeny exclusively typical—rare mutants being left out of consideration in each instance.

As between clones, differences in degree of expression of the tufted character are often conspicuous. While any clone varies from time to time in its degree of tuftedness, nevertheless, some clones have always during a term of years displayed a very large proportion of tufted branches—running, say, from two thirds to nine tenths or more. Others, growing during the same period in similar soil, in the same Wardian case, and subject, so far as possible, to precisely similar conditions, have shown only once or twice in a long life a few, possibly only one or two, distinctly tufted branches. Facts like these indicate that fixed hereditary differences, expressing themselves in differences in degree of tuftedness, exist between tufted clones.

The character of a clone may be indicated by the percentage which the total number of observed tufted branches bears to the total number of branches constituting the clone at the times at which a series of observations were made. Since this figure is based upon estimates and since the character of a clone varies, presumably in response to environmental changes, the absolute percentages calculated are not to be taken too seriously. They do, however, give a rough measure of inherent differences. Percentages so obtained range from a small fraction of one per cent. to as high as 98 per cent. One hundred per cent. tuftedness is never found; no tufted clone, living for a considerable period, has failed to produce at least an occasional typical branch. Tufted clones, then, constitute a series of an indefinite number of terms, ranging from almost complete tuftedness down to transitional types in which the distinction between tuftedness and nontuftedness is necessarily subject to error.

For some years experiments have been under way to test the effect of selection within tufted clones. In one series, a highly aberrant branch of each tufted clone was selected. This branch, isolated, served as the starting-point of a new clone. After the new clone had grown for some months, one of its most markedly tufted branches was similarly isolated, and the process has been repeated in various lines from eight to twelve times. In a parallel series, beginning with the same parental clones, a selection was similarly made in each instance of a strictly typical branch.

The result of these experiments was the production of clones which, growing for say six months, produced in the one series an increased proportion of tufted branches, and in the other series, an increased proportion of typical branches. Vegetative selection within a clone was to this extent effective. But when selection was suspended for from fourteen to seventeen months, the clones, representing the seventh or eighth selection in each line, growing and being transplanted from time to time, both those of high and those of low tuftedness reverted toward the average condition of the original parental clone. Intraclonal selection had not resulted in a lasting genetic change.

The question, however, arises how the apparent *temporary* change in character could be effected by selection. With this temporary effect of selection may be correlated the observation that a large tufted clone commonly includes patches, some of distinctly tufted, others of strictly typical, branches. Doubtless the expression of the tufted character is conditioned or affected by the environment. But in a three-inch pot of well-mixed soil, in all parts equally illuminated and equally moistened, it is difficult to explain the patchwork condition just described by localized differences in environment alone. Both the tendency to a patchwork arrangement and the temporary effects of selection indicate that a tufted branch tends more strongly to produce new tufted than new typical branches, and that a typical branch within the same clone similarly tends more strongly to produce new typical branches. To this behavior, also, analogies are to be found among angiosperms; see, for example, Darwin's classical discussion of bud variations, and Stout's study of variegated clones of Coleus.

It would be rash at present to attempt to formulate the difference in cellular constitution which, existing between a tufted and a typical branch, must supply the basis for a temporary difference in their (vegetative) reproductive behavior. Whatever the difference, it is superposed upon a fundamental and persistent genetic identity. The temporary difference may *possibly* be referable to some feature of cytoplasmic structure, which ultimately yields to the regulative action of the chromosomes.

It has been noted that genetic differences of a permanent nature seem to exist among tufted clones. To test the reality of such differences, matings have been made involving nontufted, little-tufted (1 to 12 per cent.) and much-tufted (55 to 93 per cent.) clones. The results of these matings, as determined by the characters of the f_1 gametophytes, are here presented in much-abridged form. Fuller details are embodied in a report now in press.

The possibility of error in the determination of genetically slightly tufted clones has already been alluded to. The danger of such error is greater in the classification of male than of female clones, because a larger proportion of males succumb comparatively early. With the qualification, therefore, that some errors of this type have undoubtedly occurred, the following results are presented.

Generally speaking, the more highly tufted parents produce on the average the more highly tufted offspring, less tufted parents less tufted offspring. While this is true in terms of averages, the individual clones of any family show a wide range in their proportion of tuftedness. One family (24) may be selected as illustrative. The average tuftedness of the mother was 6 per cent.; of the father, 12 per cent. The f_1 clones whose character was determined with some confidence included 37 nontufted and 38 tufted females, 14 nontufted and 12 tufted males. The degree of tuftedness among f_1 females ranged from less than one to 39 per cent.; among f_1 males, from 15 to 90 per cent. The average tuftedness of all tufted females was 11 per cent.—about twice that of the mother and approximately equaling that of the father. The average tuftedness of all tufted males was 44 per cent.—seven times that of the mother and nearly four times that of the father. The average tuftedness of all females, including nontufted, was 6 per cent.; that of all males, 20 per cent. The occurrence and distribution of so varied conditions within a single family fit the conception previously formulated of the existence of genetic differences between different tufted clones, leading to complexity in the method of inheritance of tuftedness.

The apparent intra-tetrad distribution of characters among the offspring of three types of matings involving tuftedness is shown in Table III. In this table was included every tetrad of which even a single spore gave rise to a clone whose character was determined. Thus, in the first column of the table tetrads are included which gave rise to but one or two nontufted females or to one or two tufted males.

TABLE III

APPARENT INTRA-TETRAD DISTRIBUTION OF OFFSPRING OF MATINGS INVOLVING TUFTEDNESS

(t. = tufted; nt. = nontufted)

Parents	2 ♀ nt., 2 ♂ t.	2 ♀ t., 2 ♂ nt.	Other tetrad groupings
Nont. × Much-t. (4 matings)	30	32	28
Little-t. × Little-t. (2 matings)	36	35	
Little-t. × Much-t. (1 mating)	6	8	1

Most of those tetrads produced by matings of nontufted × much-tufted that are classed under "other tetrad groupings" would fall into either the first or the second class in Table III if certain clones determined as nontufted really were genetically tufted. It is probable that in some proportion of these tetrads such a correction should be made. The class of "other tetrad groupings" includes, however, some tetrads three or all of whose spores bore the tufted tendency; possibly some tetrads three or all of whose spores were genetically nontufted, and apparently a few four-type tetrads.

The one instance among "other tetrad groupings" derived from a mating of little-tufted × much-tufted was apparently a four-type tetrad.

If tuftedness were inherited as though determined by a single factor, a mating of nontufted × tufted would be expected to yield tetrads of the two classes shown to be present in largest numbers, plus possibly some four-type tetrads. On the same basis, a mating of tufted × tufted would be expected to yield only tufted offspring. The odd fact indicated by Table III is that the matings therein included of tufted × tufted gave results agreeing more closely with the expectation, on a simple genetic basis, from matings of nontufted × tufted than did the results of the latter matings themselves.

In contrast, families derived from two much-tufted parents agreed closely with expectation. The offspring of five matings of this type were all, or almost all, tufted. Apparent exceptions were one female, a polycladous mutant in which tuftedness may have been masked by polyclady; and three apparently nontufted males, any or all of which, for reasons already given, may have been genetically tufted. The remaining 84 females and 42 males were unquestionably tufted.

These results, taken together, confirm the conclusion derived from other evidence that tufted clones may differ genetically. Stated in factorial terms, this implies that tuftedness is or may be due to several distinct factors, some or all of which are cumulative in their effects. But such multiple factors alone will not account for the intra-tetrad distribution of characters in the various types of matings described. An explanation offered in another place, postulating in addition complementary factors and certain linkage relations, fits fairly well the facts now available. This hypothesis need not be detailed here. It involves several assumptions, unfounded save as they were made to fit a complicated state of facts. The hypothesis may be somewhat simplified if it can be supposed that, as in the case of the semisterile and cupulate characters already discussed, certain factors contributed by a male parent may disappear or be inactivated in the offspring. It is true that not all paternal factors basic to tuftedness can be assumed always to be inactivated, for tuftedness has appeared among the progeny of nontufted mothers and tufted fathers. The suggestion of a maternal influence upon the expression of this character thus remains a mere suggestion, justified, however, by the observed fact that among the relatively few characters, sporophytic and gametophytic, yet experimented with, a surprising proportion, as pointed out earlier, evidence some preponderant influence on the part of the mother.

Possibly it may be permissible here to note that the behavior in inheritance of tuftedness does not, in itself, suggest the dependence of that character upon any number of specific, separable factors. The picture presented by the facts now known is that of a continuous series of genetic states ranging from the complete absence of tuftedness to its almost, but never quite, universal distribution over a clone of indefinite extent. The question might be posed whether, in dealing with a character of this nature, a factorial hypothesis can ever offer more than a purely formal explanation.

V

The results here presented, though incomplete, serve to indicate that the genetic behavior of different organisms may in important respects be very diverse, even though in other respects far-reaching similarities appear between forms so far apart phylogenetically as bryophytes, flies, angiosperms and mammals. It follows that a comprehension of the facts of inheritance and variation, and a recognition of the fundamental features of their mechanism, require the assemblage of information from all available sources, including adequately representative members of all plant and animal phyla.

THE ORGANIC WORLD AND THE CAUSAL PRINCIPLE[1]

By Professor HOWARD C. WARREN
PRINCETON UNIVERSITY

SOME thirty centuries ago a Hebrew sage summed up the outcome of his observations by declaring that "there is no new thing under the sun." In those days man's knowledge of nature was absurdly limited. A contemporary critic might perhaps have challenged the dictum, but a final decision could not then be reached. As a matter of fact, Solomon, in those words, set forth a problem which has haunted the thinking man even to this very day. We are still asking the question: Does anything really new ever appear in the universe?

Taken superficially the statement is manifestly untrue. New aggregations of atoms are constantly taking place. Every fresh geological stratum, every individual organism, whether plant or animal, every chemical compound, is a new construction. But on the other hand, science is constantly demonstrating that these apparent novelties result, one and all, from the operation of certain general principles which hold throughout the entire known universe and which seem to have held throughout all time. The problem, as I see it, is really this: Granted that the material world is constantly changing, granted that all changes proceed according to certain rigid causal principles which we call the laws of nature and that these principles hold throughout the physical universe, we must ask: Has there appeared in the course of history any *new* principle—any mode of activity which is more than a direct corollary from these universal and eternal principles of cause and effect?

The answer is still very much in doubt. Those who incline to a mechanistic view of nature generally accept Solomon's conclusion. Vitalists and teleologists take the opposite position. They assume that new forces have somehow been brought into existence with the advent of organisms and conscious beings into the world. And there has recently come into prominence another conception of things, the theory of emergent evolution, which may take either a vitalistic or a mechanistic form, but which distinctly challenges the ancient aphorism. This theory also declares emphatically that new and unpredictable properties come into being from time to time as new systems of material units are generated.

With the vitalistic conception I have never had much sympathy. It may reasonably be assumed that most of the novelties which seem to emerge in the course of evolution are not strictly novelties at all—that the laws which govern the activities of these higher complexities of matter might have been formulated in advance, as corollaries from the fundamental causal principles. This remains for future experiment and logic to settle. What I wish to point out this afternoon is that the advent of the organism and its evolution have apparently given rise to two new principles of activity in the universe—principles which, so far as I can see, are not in any way deducible from the universal laws of causation. To this extent the conception of emergent evolution seems justified.

The various laws of cause and effect, so far as they have been discovered and formulated to-day, may be summed up, I take it, under the general principle of the conservation of energy. This principle is by no means self-evident. To the casual observer every activity requires expenditure of energy; in other words, work or effort seems at first sight to involve the disappearance of a certain amount of energy. It required the most delicate experimentation to demonstrate that the energy in question is not actually lost, but is merely transformed. However, the truth of the principle of conservation seems now well established. The total effect is believed to be exactly equivalent to the sum total of the causes; in every change that occurs, the total consequents are exactly equal to the total antecedents. This principle might appropriately be termed the law of the unvarying total.

---

[1] Address of the retiring vice-president and chairman of Section I—Psychology, American Association for the Advancement of Science, Des Moines, December, 1929.