the second is the way in which varieties are known to arise in horticulture and arboriculture.

Since the publication of my book on the mutation theory (1901–3) numerous instances of mutation have been observed by different investigators among animals as well as among plants. Half a dozen species of Œnothera, some types of Primula, the walnut, the sunflower, Narcissus, Antirrhinum, Ligustrum, and many other instances might be cited. Among insects Morgan and his pupils have described more than a hundred mutations from the fruit-fly, Drosophila. Other cases have been studied by Tower for Leptinotarsa, etc.

The production of new races of agricultural crops by means of continual selection constituted for Darwin one of his strongest arguments. He showed conclusively that new species and varieties are produced in Nature in the same way as agricultural novelties. But at that time the practical method was far from being clearly understood. The work of Hjalmar Nilsson and Hays has since shown that selection may be conducted according to the principle of the mutation theory, only one choice being necessary to start the whole new variety.

It is now generally conceded by mutationists that the initial change takes place in the production of the sexual cells before fecundation. From this conception it follows that the chance of two similarly mutated cells to meet one another in this process must be very small, whereas ordinarily the mutated cells will combine with normal ones. This must produce half-mutants, and these may, in ordinary cases at least, split off the full mutants after the same rules which Mendel discovered for his hybrids. Sometimes the half-mutants will be distinct from their ancestors, as in *Oenothera Lamarckiana rubrinervis* and *erythrina*, and, therefore, will easily be discovered. In other instances external differences may be absent, and only the unexpected production of a new type in about 20–25 per cent. or more of the individuals will betray the internal change. This explains the mass-mutations discovered by Bartlett. Such an indirect way of producing mutations by means of two successive steps seems to be very common in Nature, and will probably afterwards prove to be the general rule.

Willis has made an elaborate statistical study of the appearance of endemic species, which he considers to be the youngest of their region. He finds that utility of the new characters cannot have had any part in their production, since it cannot be shown to have any influence either on their first local extension or on their subsequent spreading over larger regions. Wide spreading is mainly the result of age, the oldest species having, as a rule, the largest areas. Moreover, in comparing the diagnoses of endemic species with the differences among the mutated forms of such a group as the evening primroses one finds a close parallelism, showing that our experimental mutations are quite analogous to the species-producing steps of Nature.

Objections against the mutation theory have been made by different investigators. Some systematists and palæontologists still adhere to the old view either wholly or only for special cases. Biologists rarely attack the theory in a direct way, but mainly discuss the question whether the observed mutations are really the representatives of the species producing changes in Nature, as is claimed. They assume that the splittings seen in our experiments are due to hybridism, and that every mutating species is a hybrid between supposed ancestors which possessed the mutative characters as specific marks. This idea can scarcely aid in simplifying the question, since it puts the origin of the characters involved on to unknown parents. Sterile varieties cannot produce hybrids, and therefore cannot originate in this way. This fact seems sufficient to disprove the hypothesis. In the case of the evening primroses this view has led to fantastic diagnoses of hypothetical ancestors, but even these fail to explain the facts observed in our cultures. Morgan's hypothesis of crossing over, which goes far to explain the splitting phenomena of the fruit-fly, fails in its application to the evening primroses, since here half-mutants are the rule. These must evidently be produced without the aid of that process. Moreover, the heterogamous mutants have dominant characters which are handed down by the egg-cells, and not by the pollen, instances of which are given by the mutations called *lata, scintillans, cana, liquida,* and others of *Oenothera Lamarckiana.* Evidently these can never be explained by the assumption of a hybrid condition of the parent species.

Thus we see that the broad arguments for the mutation theory are continually increasing in number, whereas the criticisms are more and more directed against special cases. They are concerned with the possibility of experimental proof and with the fitness of our material for further studies, but are not expected to invalidate the theory as such.

THE PROGRESS OF MENDELISM.

BY PROF. W. BATESON, F.R.S.

FROM the discoveries to which the Mendelian clue immediately led, many lines of research and speculation are diverging. These enterprises have still aims in common, a fact which we recognise by including all under the one name, genetics; for, though various in their methods, all relate to the physiology of breeding, a department of science the growth of which is a feature of the period surveyed on this occasion.

Stocktaking at the present moment is, however, not easy. Much of the new work is in an incipient stage, and that which is the most attractive of all—namely, Morgan's effort to establish a close connection between cytological appearances and the results of experimental breeding—promising though it is, must be tried by tests on a scale far wider than experience of Drosophila provides before we are able to assess its value with confidence. Whether the theory that the factors are arranged in the chromosomes, like beads on a thread, stand or fall, it has already served the purpose of a good theory. It has fired the minds of many workers, and has directed their inquiries with manifest success. Its weakness lies first in the narrowness of the field studied, but besides this it is not yet wholly free from the objection that the subordinate and incidental hypotheses are not altogether independent of each other.

Various as are the methods of attack, the objects before us are sufficiently clear. Among them the most important is a determination of the moment or moments at which segregation may occur. To the solution of this problem most of the investigations contribute. On one hand, we have the large body of facts consistent with Morgan's view that synapsis is the critical moment. Were our outlook confined to animals, we should scarcely hesitate to accept that hypothesis as satisfying the conditions, but the plants give no such clear answer. Not only is an obvious somatic segregation leading to genetic diversity of the parts not rare, as in many variegated plants and plants which give dissimilar forms from adventitious buds, but there is now a large group in which the male and female organs of the same plant differ in the factors which they carry. Miss Saunders's stocks are the classical example, where the male side carries doubleness and cream plastid colour, whereas the ovules are mixed in these potentialities. Similar sex-linkage, as, following Miss Pellew's use, it may provisionally be called, has been shown to exist in Petunia, *Campanula carpatica, Begonia Davisii,* and in certain forms of Œnothera.

In all such examples segregation cannot be supposed to occur later than the constitution of the sexual organs. Collins's experiment, showing that in Funaria the scales surrounding the male organs by their vegetative growth give rise exclusively to male mosses, is another and very striking indication to the same effect. The genetics of "rogue" peas point to a similar conclusion in regard to the distinction between the rogues and the type from which they come. In some way not yet clear, the type-elements are wholly or partially excluded from the germ-lineage of the heterozygotes, being apparently relegated to the lower parts of the stem. Such facts raise a suspicion that, considered as genetic machines, plants may be fundamentally distinct from animals, an idea already suggested by the contrast between their modes of growth. In the animal the rudiments of the gametes are often visibly separated at an early embryonic stage, whereas in the plant they are given off from persistent growing points. Indeed, since Baur's work with variegated chimæras, which led to his brilliant interpretation of Winkler's "graft-hybrids," this possibility has inevitably been present to our minds.

In knowledge of the nature of sexual difference many very substantial advances have been made, which have much extended the original discovery that sex depends on a segregating Mendelian factor, in some forms the male, in others the female being the heterozygous member. In the fowl femaleness is dominant, and the hen is heterozygous in sex, from which Morgan drew the interesting corollary that the "henny" character of the Sebright cock is also a dominant. Not only has this been proved experimentally, but he has lately shown that after castration the Sebright cock acquires ordinary cock's plumage, much as hens do in ovarian disease. Perhaps we may regard the henny male as containing part of the large compound factor which normally constitutes femaleness. Conversely, we may interpret the spurs frequently present in normal Leghorn hens as indicating that they have lost that part of the female factor which inhibits the growth of the spur. Whether such transference involves actual detachment of chromosome material, as Morgan's theory would demand, is uncertain. Nevertheless, an approach to such evidence is provided by the extraordinarily interesting observation of Bridges of a condition which he calls non-disjunction. Certain crosses in Drosophila failed to exhibit the normal sex-limitation, and unexpected terms appeared. Bridges was able to show that in the families which behaved in this way an extra sex-chromosome sometimes occurred, carried over, as he imagines, by some error of division. Not improbably Doncaster's female-producing strains of *Abraxas grossulariata,* in which evidence of an extra chromosome was found, are an analogous case. Patterson with great probability proposes a similar explanation for the curious phenomenon which he has investigated in Copidosoma, where, by polyembryonic division of a single egg (almost certainly), males, females, and inter-sexes may result. The inter-sexes seen by Kuttner in Daphnia, and those produced by J. W. Harrison with considerable regularity in some hybrid combinations of species of Geometers, are obviously to be considered in this connection, and doubtless the sterile males, accompanied by fertile females, which Detlefsen found as the normal produce of a species cross in Cavia, will be investigated with such possibilities in view.

But though sex behaves in so many ways as a Mendelian allelomorph, showing, of course, frequent phenomena of linkage, it begins to be remarkable that no case of crossing-over in respect of these linkages has yet been established. Were the sex-chromosome always mateless, this fact would fit admirably with Morgan's views, but since the *x*-chromosome not rarely has a mate, a distinct problem is created. As bearing on the same question, we have also to remember Tanaka's observation that a certain linkage found in the male silkworm is absent in the female.

Another far-reaching discovery has been made by F. Lillie. When in horned cattle twins of opposite sexes occur, the female is sometimes sterile, being called a free-martin. We were inclined to interpret these twins as arising by division of one fertilised ovum, but Lillie, in a study of material from the Chicago stockyards, found that an ovum had dehisced from each ovary, and the twins were therefore originally distinct. Moreover, he showed that in some instances the twins have an actual anastomosis in the fœtal circulation. We are thus driven to believe that the presence of a male embryo may influence—in cattle—the development of a female embryo, poisoning it, in so far that the development of the generative organs is partially inhibited.

Many complex cases of interaction between factors have been successfully analysed. Punnett's elaborate experiments on the colours of rabbits and sweet peas, Emerson's studies in Phaseolus, and several more such investigations are gradually laying a solid foundation from which the mechanism of factorial determination may be deduced. The discovery made by Nilsson-Ehle, and independently by East, that in some forms there are several factors with identical powers, is another notable advance.

Controversy is proceeding respecting the divisibility of factors. When on segregation, either in the gametes of F_1 or in later generations, instead of two or three sharply differentiated classes of zygotes, much intergradation occurs, or when one of the parental types fails to reappear, the result may be interpreted either as showing imperfect segregation, or as an indication that the number of factors involved is very large. The balance of evidence perhaps suggests that many factors can, and on occasion do, break up (as the sex-factor almost certainly does), some commonly, others exceptionally, while others, again, seem to maintain their individuality indefinitely unimpaired.

As bearing on evolutionary theory, the new work leaves us much where we were. Progress in genetic physiology has been rather a restraining influence. The notion that Mendelian segregation applies to varieties and not to species has been often refuted. One of the most useful contributions to this subject is Heribert-Nilsson's evidence respecting Salix hybrids. Wichura believed himself to have proved that they and their derivatives are simple intermediates between the parental forms, and this statement, which has passed current for fifty years, is now shown to be a mistake due to insufficient material. Interest also attaches to Castle's recent withdrawal of his conclusion that by continued selection certain Mendelian characters in rats could be modified, an opinion which, though consistent with his own experimental work, has not stood a crucial test. We are still without any uncontrovertible example of co-derivatives from a single ancestral origin producing sterile offspring when intercrossed. This, one of the most serious obstacles to all evolutionary theories, remains. The late R. P. Gregory's evidence that tetraploid Primulas, derived from ordinary diploid plants, cannot breed with them, though fertile with each other, is the nearest approach to that phenomenon, but the case, though exceptionally interesting, does not, of course, touch this outstanding difficulty in any way.

Space does not suffice to enumerate the practical applications of genetic science to economic breeding, of which some have already matured and many are well advanced.

TELEGONY.

By PROF. J. COSSAR EWART, F.R.S.

THE belief in telegony is probably as old as the belief in maternal impressions, so intimately associated with Jacob's breeding experiments, recorded in the thirtieth chapter of the Book of Genesis. In prehistoric times, when breeds of sheep and cattle brought from the East by the Alpine race were crossed with the more recently formed European breeds striking new varieties would now and again appear. The ancient shepherds would doubtless endeavour to account for the differences between the cross-bred offspring and their pure-pred ancestors, and later biologists would be called upon to decide which of the views of the ancient breeders were most worthy of support.

The doctrine of the infection of the germ now known as telegony was more or less firmly believed in by men of science as well as by breeders up to the end of the nineteenth century. Beecher, writing at the close of the seventeenth century, says: "When a mare has had a mule by an ass and afterwards a foal by a horse there are evidently marks on the foal of the mother having retained some ideas of her former paramour, the ass." Agassiz held that the ovary was so modified by the first act of fecundation that "later impregnations do not efface that first impression." Similar views were entertained by Haller, Darwin, Herbert Spencer, Carpenter, Sir Everard Home, and others, and up to 1895, when I started my experiments, physiologists as a rule either admitted the possibility of the blood of a mare imbibing from that of the fœtus some of the attributes which it had derived from its male parent and thereafter handing them on to offspring by a different sire, or believed that some of the unused germ plasm