CHAPTER VII

SOME DISPUTED QUESTIONS

In this chapter will be briefly considered certain questions which either are still quite unsettled, or upon which there is still active disagreement among biologists. It will be convenient to take first some which are closely connected with the Mendelian theory of heredity, and pass on later to others which are related equally to any theory of inheritance which may be adopted.

One of the chief lines of attack on the Mendelian theory has been the proposition that the absolutely complete segregation of allelomorphic characters in the germ-cells, postulated by that theory, has not been proved. If the theory is rigidly true, then in the case of a tall pea crossed with a short (Chap. V) the homozygous talls and shorts among the offspring of the cross should be as pure for tallness or shortness as the original parents; neither character should have been influenced in any way by its association with the other. It has been maintained that the Mendelian categories are not sufficiently definite to allow such a statement to be made with certainty. The Mendelian can only reply, that in the great majority of cases the 'extracted' pure individuals in the F_2 generation do not differ recognisably from the original parents in the characters considered, and that no signs of impurity can be found in later generations.

There are however instances in which it appears that Mendelian segregation may not be perfect. It has been maintained that an instance of this is provided by hair-length in guinea-pigs. When a long-haired ('Angora') guinea-pig is mated with a short-haired, the F_1 offspring are short-haired, shortness being dominant, owing perhaps to the presence of a factor which prevents the growth of the hair after reaching a certain length. But when such F_1 (heterozygous) short-hairs were mated together, in addition to apparently pure longs and shorts, animals with hair of intermediate length were produced, and these crossed back with pure long-hairs gave no short-haired young. It is suggested that the long and short characters have become fused in some germ-cells, segregation being incomplete or non-existent, so that germ-cells bearing the mixed character are produced. Again, in a cross between lop-eared and short-eared rabbits, young with ears of intermediate length are produced, and these mated together give no evidence of segregation in the next generation. From these and some other similar observations it must be concluded, either that in some cases there is incomplete segregation or even complete fusion of alternative characters, or that what appear to be simple characters are really complex, and that the true-breeding intermediates are formed by a new combination of elementary factors. An instance, which is perhaps similar, will be mentioned in the next chapter in discussing the inheritance of pigment in Man.

A second question with regard to Mendelian segregation has at present received hardly any answer, namely, whether the apparently 'continuous' variations such as were illustrated by the example of Johannsen's beans (Chap. IV) segregate according to the Mendelian rule. It was seen that each 'pure line,' derived by self-fertilisation from an individual plant, has its own type about which the size of the beans borne by the plant fluctuates; but it is not known whether, when two plants having different types (modal sizes) are crossed, segregation takes place between the two types in the formation of the germ-cells of the crossed individual. To determine this would naturally require a long and difficult series of experiments, and at present very little is known of the subject, but when it is remembered how widespread and in what varied characters segregation has been found, it would not seem improbable that it should occur in such cases also.

Another subject which Mendelian investigation has brought into prominent notice, and which has led to much controversy, is the kind of variation which has been effective in the process of evolution. Darwin assumed that evolution takes place by the preservation of very small 'continuous' variations which occur in a direction favourable to the species, but even among his immediate followers, for example Huxley, doubt was expressed whether larger step-like variations or 'mutations' may not have been operative. Darwin rejected this idea chiefly on the ground of the rarity of such mutations, which makes it inevitable that the mutating individual should generally mate with one of the normal type, and so it was supposed that the mutation would be diluted and rapidly lost. But Mendelian work shows that this dilution does not occur in simple cases; the offspring of the cross between the mutation and the type produces half its germ-cells bearing the mutation to its full extent, *and these will transmit the mutation until the race* may become widely infected with it, and not infrequently individuals both of which possess it will mate together. If the mutation be dominant, as in the case of the well-known black variety of the 'Peppered

Moth' (*Amphidasys betularia*), it may spread rapidly until it becomes common, and if recessive it will equally often be represented in the germ-cells of many individuals and will appear when two which bear it mate together. In either case if the mutation be advantageous it may be preserved at the expense of the type by natural selection, until it obtains a firm footing. But the difficulty has naturally been felt that the marvellously perfect adaptations which are so frequent in nature cannot be imagined to have arisen by large steps, but must have been acquired gradually, and therefore many naturalists reject the suggestion that mutations can have been largely operative in evolution. But the fallacy here is the assumption that all discontinuous variations must be large; the case of Johannsen's beans shows that essentially stable variations occur, which probably differ from mutations only in their small extent, and by the selection of such 'minute mutations' the wonderfully perfect structures of living things might be produced. It may perhaps be regarded as hair-splitting to distinguish between minute mutations and fluctuating variability, but the distinction lies in *the nature of their inheritance, which is the essential* thing in evolution. It has been seen that no selection within the 'pure line' in the case of the beans has any effect; for progress to be made, a new mutation, small though it might be, is necessary.

The problem in heredity which has probably given rise to more controversy than any other is that alluded to more than once previously, of the inheritance or non-inheritance of acquired characters, that is, characters produced in the individual during its life by the action of some sort of stimulus. Some aspects of the question have already been considered, and from what has been shown of the very definite nature of the inheritance of germinal (inborn) characters, it will be understood why students of heredity are increasingly disposed, *a priori*, to disbelieve in the transmission of acquirements; for if these were transmitted to any considerable extent, this fact must interfere, one would suppose, with the orderly appearance in the offspring of the characters represented in the germ-cells of the parents. But at the present time no treatment of heredity could be regarded as complete without some mention of the evidence which has been adduced in favour of the transmission of such characters. Unfortunately, the evidence is almost always capable of interpretation in more than one sense. The supporters of the belief in transmission rely largely on indirect evidence, especially on the difficulty of imagining any cause of evolution in certain directions if the effects of acquirement are excluded. A vast literature has grown up around this question, of which only illustrative examples can be given. In animals which live in the dark the pigment in the skin is frequently absent, as it is also in flat-fish on the side of the body which lies protected from light on the sea-floor. It is said that pigment in such cases cannot be harmful, and so its disappearance is not due to natural selection. *But pigment very generally appears in response to* the action of light, and so it is supposed that the absence of the stimulus to production, acting for many generations, has caused the pigment to disappear. This is illustrated by the well-known experiment of Cunningham on flat-fish. The young *fish is pigmented on both sides of the body; it* then settles on one side and the pigment on that side disappears. Cunningham reared such young fish in an aquarium lighted from below: when they settled on the bottom the pigment disappeared, but if kept still longer exposed to light from beneath, *the pigment began to come back again.* The disappearance of the pigment, although exposed to light, proves that the loss is hereditary; its return on continued exposure to light is interpreted by Cunningham to mean that its disappearance was due to absence of light, and has gradually become hereditary, *but that the process can be reversed by* again exposing the lower side to the action of the stimulus. The same argument has been used with regard to the colourless skins and vestigial eyes of animals living in caves; where the structure is use-less it disappears, and the most obvious cause to assume is lack of use, which, acting cumulatively through many generations, has become hereditary. Such evidence, however, is only presumptive, it does not amount to proof, and on the other side may be adduced the pigments of birds' eggs. Birds which nest in holes or dark places usually have colourless or slightly coloured eggs, while those which lay in open places have eggs more or less matching their surroundings. This appears closely comparable with the condition of skin-colour in fishes and amphibians, and yet it is impossible that the action of light could have any direct effect on the production of pigment in birds' eggs. That the loss of pigment in each case is connected with its uselessness is probable, but the birds' egg case seems to show that it is not due to 'use-inheritance.'

A second instance of the indirect evidence for the inheritance of acquired characters may be given, that of instinct. Instincts are very similar to firmly rooted habits, and have been regarded as habits which from being performed through many generations have become hereditary. There can be no doubt that, in the higher animals especially, instincts may be reinforced and perfected by habit, but many cases can be adduced in which it seems impossible that habit has played a part in the evolution of an instinct. Many insects have exceedingly perfect and complex instincts in connexion with egg-laying, yet the process may last only a few hours, and the eggs may all be fully formed and ready for laying before the insect hatches. In the worker-bee, too, there are many admirably developed instincts, and also structural features which might be thought to have originated by the transmission of acquired adaptations, and yet the worker-bee, except in rare cases, never reproduces itself, but is produced by a queen and a drone with structures and instincts different from its own. If in these cases we find perfect instincts which cannot have arisen by the inheritance of acquirements, it seems unreasonable to assume that instincts in other species must have arisen in this way. These two cases are given merely as examples of the presumptive evidence that has been brought forward. It is admitted that the process of evolution would be more easily comprehensible if the inheritance of acquired characters were a fact, but it is clear that no absolute proof of its existence can be based on cases of this kind.

Exact experiments on the possible inherited effects of acquirements are difficult to devise so as to be unequivocal, and most have given negative results[1]. A case which at first sight seems to prove

[1] Experiments on moths and butterflies have been mentioned in Chapter III; in some, notably those of Fischer with the Tiger Moth,

the inherited effects of conditions is the experiment of Kellogg in starving silkworms, in which he found that when the caterpillars were starved for two generations, the third generation, even if well fed, were below the normal size. But there is here a possible source of error, that the eggs produced by starved females may have been lacking in yolk, so that the resulting caterpillars would be weakly from the beginning and never overtake the normal size. If so, the apparent effect of inheritance of bad conditions would be due really to poor embryonic nourishment, not to germinal difference. The same explanation might apply to the apparent cumulative effects of under-feeding in man, if the mother cannot adequately nourish the infant before birth. The famous experiments of Brown-Séquard on the inheritance of artificial injuries in guinea-pigs must be mentioned. He found that when the parents were subjected to operations of various kinds, some of the young showed corresponding abnormalities, especially in the case of the effects of certain injuries to the nervous system. Subsequent experiments however have not completely confirmed his results, and there is reason to believe that where they have

Arctia caja, definite evidence for the transmission of modifications was obtained, but this may have been due to direct modification of the germ-cells themselves.

been confirmed there are other possible explanations of the apparent transmission of the effects of injury. For example, Brown-Séquard found that when the chief nerve of the leg is severed, the toes become morbid and the animals frequently nibble them away. A small percentage of the offspring of guinea-pigs lacking toes from this cause also had toes missing. But it has been pointed out that rodents in captivity sometimes eat off the toes or tails of their young, and if the mother had acquired the habit of nibbling her own toes, she might bite off those of her young shortly after birth and give the appearance of the inheritance of a mutilation [20, 29]. Evidence has also been brought forward that the mutilation of the parents may cause the production of a toxin, which is transmitted directly to the offspring, and causes abnormalities to appear in them in the same organs that were injured in the parent.

Quite recently Kammerer [19] in Vienna has made some remarkable observations on salamanders and a species of toad which seem to support the idea of the inheritance of acquired characters. For example, among other experiments, he finds that the animals can be accustomed to lay their eggs in water instead of on land, and the young become modified to suit their new surroundings, and the modifications are progressively increased in later generations. He points out however that most of his results, like those obtained by Tower (Chap. III), may have been brought about by the action of environment on the eggs at the time of maturation, but they differ from Tower's in the regularity of their appearance and in being adaptive. Further work in this direction will be awaited with interest[1].

[1] Reference must also be made to the work of Sumner [32 *a*] who finds that rats kept at a high temperature differ in several particulars (proportions of the body, etc.) from those kept in a cold room. These characteristics are inherited to a measurable extent, and the explanation offered in the case of insects, that the germ-cells were directly affected by the temperature, is not easy to apply to a warm-blooded animal. There may of course be indirect effects, brought about by a change in general constitution, but the admission of this hardly differs from accepting the inheritance of acquired characters. A considerable list of cases of the transmission of environmental modification, chiefly but not entirely in plants, is given by McDougall [22 *a*]. An important contribution to the subject is the recently published work of Boas, reviewed in *Nature*, Nov. 3, 1910, p. 11. He finds from a study of the children of European immigrants into New York that whatever the racial characters of the parents, the children born after their arrival in America tend to approach a certain type, and approach it more nearly, the longer the parents have lived in New York. For example, the children of a long-headed race have progressively shorter and rounder heads, the longer the parents have lived in America before their children are born, while those of round-headed parents become longer so as to approach the same type. In this case there is no question of the inheritance of 'acquirements' in the ordinary sense, for the shape of the parents' heads is not affected; it appears that either the germ-cells or the young children themselves are affected in such a way as to cause them to approach a characteristic American type in head-shape and other characters.

On the whole, the hypothesis of the inheritance of acquired characters must be regarded as 'not proven,' and our increasing knowledge of the definiteness of many germinal characters makes it doubtful whether it can be a factor of great importance in the constitution of the individual, or to the course of evolution. Some further evidence in this direction will be given in the next chapter[1].

A few minor questions remain. One of these, which has played a considerable part in biological literature, is the alleged phenomenon called Telegony.

[1] The recent evidence which has been brought forward on the subject warns us against a dogmatic denial of the possibility of the inheritance of acquired modifications. The number of cases recorded is now considerable, in which adaption to changed environment, either of structure or instinct, appears to be transmitted to the next generation. The tendency of biological thought is certainly towards a recognition of the unity of the organism as a whole, including its germ-cells, and especially where the organism adapts itself to change, it seems possible that this adaptation is transmissible. The belief that 'somatic' changes could not be transmitted rests largely on the idea that every character is determined by a 'factor' or determinant in the germ-cell, but it is clear that any character is not developed directly from the germinal determinant, but by the relation existing between the determinant and its surroundings, viz. the body of the organism. If the surroundings are changed, this relation may be altered, and the altered relation may be transmitted to the offspring, so bringing about a corresponding change in the character as it appears in the next generation. How far such changes are of real importance, and whether they are permanent or, so to speak, temporary expedients to meet changed conditions, is still an open question. Students of heredity generally would take the latter view.

It was formerly believed, and the belief is still firmly held by fanciers and animal breeders, that if a female of one breed bears young by a male of another breed, and is then mated with a male of her own kind, the offspring of this second mating will in some cases show the influence of the first sire, and instead of being pure-bred will in some respects be mongrels resembling the mongrel offspring of the first mating. The instance of this made classical by Darwin is 'Lord Morton's Mare,' in which a chestnut mare bore a colt by a quagga, and afterwards two colts by a black Arab stallion, both of which were dun-coloured, and bore stripes on the legs and in one colt on the neck also [7]. But it is known that dun horses are frequently striped to some extent, and Ewart's well-known work with zebras [11], in which it was attempted to repeat this experiment, gave negative results. The belief in telegony is widely held among dog-fanciers, and many cases could be quoted, but whenever properly controlled experiments have been made, no evidence of telegony has been forthcoming. The belief in it is almost certainly due to the habit of generalising from individual instances; whenever a case occurs which appears to favour the belief, it is adduced as proof, even though other causes may have been operative, and matings in which no evidence for it appears are passed over in silence. If it were a genuine phenomenon, it is almost certain that conclusive evidence for it would have been obtained in the numerous breeding experiments recorded in recent years.

Another idea very widely held, but apparently resting on no better evidence, is the belief in maternal impressions, especially in the case of mankind. By maternal impression is meant the influencing of the child by events affecting the mother during pregnancy. It is commonly believed that if a pregnant woman is injured in any part, or even sees an injury to another person so as to excite her imagination, the corresponding part in the child may be abnormally developed, or may bear some mark, caused, it is supposed, by an impression conveyed from the mother. More general still is the belief that the temperament of the child is influenced by the mother's mental condition during pregnancy. This latter belief is scarcely susceptible of accurate investigation, but the belief in bodily marks or malformations being due to corresponding injury to the mother, or to her attention being strongly attracted to that part, is almost certainly based on coincidence. A large number of children are born with some abnormality, and a very large proportion have some mark on the skin. Many mothers during pregnancy undergo some slight accident or see some deformed person, and thus it must happen that a mark on the child will often roughly coincide in position with the part affected in the parent. If every coincidence of this kind is quoted as proof of the reality of maternal impression, and the cases are left unheeded in which no relation can be found between abnormality in the child and events affecting the mother, it is natural that a belief in the phenomenon will easily take firm root. The evidence available however is probably insufficient to support any other view than that of accidental coincidence.