The Species Problem in the Light of Genetics.[1]

By J. B. S. HALDANE.

DARWIN held that the differences between species were due to the accumulation of such smaller differences as distinguish varieties within a species. Since the rediscovery of Mendel's papers, a vast amount of work has been done on the genetical basis of intra-specific varieties, and a smaller, but still considerable amount, on the genetics of specific differences.

Intra-specific differences, so far as they are hereditary, can be classified as due to one of the following causes :

1. Extra-nuclear 'factors', or plasmons. These are inherited entirely or almost entirely through the mother. They cause many of the differences in chloroplasts between different plant varieties, the plastids being handed on maternally as more or less independent units. They may also interact with nuclear factors to alter such characters as the development of the anthers. They are not certainly known in animals.

2. Single intra-nuclear factors, or genes. An enormous number of varietal differences, in both wild and domesticated organisms, have been shown to be due to one, or a small number of genes.

3. Multiple genes. Quantitative differences are often due to the action of a number of genes. In some cases an apparently continuous varying character can be shown by careful analysis of individuals to be determined in this way. Moreover, Fisher has shown that the correlations found for human stature between relatives by Pearson and his pupils are in quantitative agreement with expectation on the hypothesis that they are due to multiple genes.

4. Differences in the arrangement of genes within a chromosome. Sturtevant has shown that different geographical races of *Drosophila melanogaster* differ in the order of the genes in a chromosome, as determined by linkage experiments. A section of a chromosome of one race appears to have been reversed in the other. Similar results have been produced by Muller with X-rays.

5. Differences in chromosome attachment. A chromosome of one variety may be represented by two smaller bodies in another, as in *Zea Mays*, or a fragment may be attached to different larger chromosomes in different varieties, as in *Drosophila melanogaster*.

6. Unbalanced differences in the amount of chromatin. One or more chromosomes, or portions of them, may be represented once, thrice, or four or more times in a variety, as compared with twice in the type. This is not only the genetical basis of sex in most organisms, and of intersexuality and other abnormalities in some, but also occurs in varieties of other types. For example, some fatuoid oats, and most cultivated sweet cherries, have one or two chromosomes in addition to the set characteristic of the species. In this condition some genes are represented three or four times, the majority twice. This generally produces a greater effect on the visible character than results from a trebling or quadrupling of the haploid number of all the genes at once.

7. Polyploidy. The number of chromosomes is here two, three or more times as great in one variety as in the other. This generally results in an increase of size, but often the visible effect is very small indeed, far less than that of many single factors or of an unbalanced difference in chromosome number. But it invariably results in a certain degree of physiological isolation. Not only is there often difficulty in crossing a diploid and a tetraploid, but also, if the union is fertile, the hybrid is generally a triploid, and therefore much more sterile than either parent owing to irregularities in meiosis.

Differences of all these types have arisen in animal and plant races under observation, and all but the first have been produced experimentally. So far as I know, there is no clear evidence that any intra-specific hereditary variations are due to causes other than these, though it is possible that the list is not yet complete, and some of the cases ascribed to multiple genes demand much further study.

The assertion is still occasionally made that characters inherited in a Mendelian manner are pathological. This may, I take it, mean one of two things. The character may be supposed to be disadvantageous to its bearer. Much of the variation in shell pattern of wild *Cepea nemoralis* is due to two factors. Diver has shown that the four races produced by the interaction of these factors have been in existence in England since Neolithic times, and although it is conceivable that one race may have some slight advantage in a particular environmental niche, there can be no such advantage in the country as a whole, or selection would have eliminated certain of the types. Naturally, however, most variations from the normal are disadvantageous in a normal environment, and are therefore eliminated by natural selection. Many mutants are definitely shorter lived or less fertile than the type. But Pearl and his pupils have shown that in artificial conditions some of the mutant types of *Drosophila melanogaster* are more fertile than the type, others longer lived. Such mutants cannot be called pathological.

Secondly, it may be meant that a Mendelian character is pathological because it is due to injury. Mutants are produced in large quantities by X-rays, and it may be that much of normal mutation is due to the β- and γ-rays from potassium, other radioactive substances, and cosmic radiations. I can see no reason why such mutation should be regarded as more pathological than photosynthesis or sunburn. It is probably a prerequisite of evolution, and its effects are not necessarily harmful either to the individual or the species, though often so to the individual.

[1] Paper read to the Society for Experimental Biology on June 15.

Inter-specific differences are largely due to the same causes as intra-specific. In general, they can only be analysed genetically where the species can be crossed. But this is not always the case. For example, the order of the genes in the chromosomes of different species of *Drosophila* can be shown to be nearly, but not quite, the same. The linkage values of homologous genes are somewhat different in the mouse and rat. Since the yellow *Primula acaulis* and related species differ from the purple *P. Juliae* by the loss of a gene needed for anthocyanin formation, it is very plausible that other yellow Primulas also lack this gene.

Differences in chromosome number and arrangement can, of course, also be observed apart from crossing. A few examples of inter-specific differences will now be given under the same classification as that adopted for intra-specific.

1. In a number of plant species crosses, one of the F_1 hybrids is vigorous, while the reciprocal has defective plastids, and is yellow or variegated. Renner regards this as due to the inviability of the maternally inherited plastids in the presence of the hybrid nucleus. A very clear case of a plasmon causing sexual abnormality after species crossing occurs in *Geranium* (unpublished work of the late Mr. Newton). There are probably analogous cases in animals; indeed, wherever adult reciprocal hybrids of the homogametic sex differ, extra-nuclear inheritance may be suspected.

2. Mendelian segregation for some characters in F_2 is very common. Apart from cases where varietal characters of one species still behave in a Mendelian manner after the crossing, some of the actual specific characters are so inherited. Sometimes, however, the ratios in F_2 diverge markedly from expectation.

In plants the genes by which species differ often cause striking differences. Thus Chittenden showed that the purple *Primula Juliae* had no gene for plastid pigments, the primrose none for anthocyanin. Hence white flowers appeared in F_2. On the other hand, the colour genes distinguishing crossable rodent species cause rather smaller changes, and are multiply allelomorphic with genes causing the sharp differences distinguishing domestic varieties. Thus *Cavia porcellus* has a gene for yellow-bellied agouti, *C. rufescens* for agouti-bellied agouti, both allelomorphic with the gene found in the well-known black variety.

3. When species are crossed the F_1 is generally uniform, the F_2 variable, often differing among themselves more than do the parent species. This fact is, of course, the principal reason why hybridisation is employed in horticulture to obtain striking new forms The phenomena can be exactly paralleled in varietal crosses, and are probably due to multiple gene differences.

4. The order of the genes is slightly different in *Drosophila melanogaster* and *D. simulans*, and probably in other *Drosophila* species which cannot be crossed.

5. There is strong cytological evidence for this when the chromosomes of different species are compared, and fairly good genetical evidence both in *Drosophila* and mammals. Thus the gene the loss of which converts a grey mammal into a yellow is sex-linked in cats but not so in rodents, suggesting that a corresponding gene is carried by the *X*-chromosome in the cat, by another chromosome in rodents.

6. Unbalanced differences of this type between species probably occur in *Viola* and some other genera. They are not, however, quite so well authenticated as types 5 and 7.

7. This type of difference is very common in plants, and extremely rare in animals. For example, in *Rosa*, species with 14, 28, 42, and 56 chromosomes are known, besides species with intermediate numbers, which are probably hybrids.

It is obviously impossible to state that all inter-specific differences can be explained on these lines. It is, however, doubtful whether any differences are known which cannot be so explained. In view of the very great morphological and physiological differences produced by single genes, there is no reason to doubt their capacity for causing inter-specific differences of these kinds, which are often less striking than varietal differences. The stumbling-block in the past has been the failure to find, between varieties, the physiological barrier which often prevents the effective crossing of species. This failure was regarded as a serious but not fatal objection to Darwinism by such men as Huxley and Romanes. It has now been completely overcome. Let us consider, for example, *Primula sinensis* and its tetraploid variety *gigas*. Every plant of these forms in England is descended from the same few seeds brought over from China in 1819–26. The giant tetraploid form has originated on several occasions in cultivation since 1900. Tetraploid pollen on the diploid stigma has never produced a single seed. The reciprocal cross, though very extensively made, has produced about a dozen hybrids. These hybrids are often triploids, and hence have irregular reduction divisions, and are far less fertile than either parent. We have thus a complete analogy to the case of true species, and indeed some geneticists regard such tetraploids as new species. Such tetraploidy can sometimes be produced by injury of the diploid plant. This produces a tetraploid branch, and if this branch is self-fertilised, the seedlings are tetraploids. Incidentally, this is the only case known to me in which a *somatically* acquired character is transmitted by sexual reproduction.

Phenomena similar to those found in the F_2 of species crosses may be produced by the action of small numbers of genes. Thus Gonsalez found the following expectations of life in days for *Drosophila melanogaster* females. The characters are recessives and combinations of recessives two or three at a time.

Wild	40·6
Purple (eye)	21·8
Arc (wing)	28·2
Speck (axilla)	38·8
Purple, arc	32·0
Purple, speck	23·0
Arc, speck	34·7
Purple, arc, speck	40·7

Clearly this last combination represents a physiological balance as good (under the artificial culture conditions) as the normal. All other combinations are below the viabilities of the triple dominant or the triple recessive. It is well known that when species are crossed, the F_1 generation, though itself often vigorous, produces gametes and zygotes less vigorous than those of the parental types. In some cases I conceive that related species are simply those genotypes, out of a large possible number, which possess the highest viability.

I contend, then, that all specific differences so far analysed may be due to the cumulative action of known types of varietal difference. Whether they actually are so is another question, but on the principle that *entia non sunt multiplicanda praeter necessitatem*, we are justified in assuming, as a provisional working hypothesis, that they are. The question as to how species arise in Nature is a much more complicated one. Natural selection undoubtedly occurs; on the other hand, the environment may influence the rate of mutation, and it is probable that mere chance plays a certain part in establishing new types. Many other causes of evolution have of course been postulated. Which of these processes is the more important is a matter which can only be decided by observation of Nature, and not by experiment alone.

Aspects of Psychology in Education.[1]

By Dr. C. W. Kimmins.

One of the most significant of recent movements in education is the change of attitude towards the mental development of the very young child. Until comparatively recently, the physical condition of the child up to the age of six years was the only matter that appeared to need serious attention. Educationists and psychologists now, however, at long last, fully realise that the period from two to six years of age is far and away the most important of the child's life. In other words, there must be a really sound foundation if a satisfactory superstructure is to result in the child's development. The mental as well as the physical welfare of the young child must receive adequate attention. The reliable evidence we possess that many of the cases of serious mental trouble in later life may be traced to unwise treatment in early childhood is a case in point. During this period of active habit formation, when the necessary sublimation of nascent instinctive impulses is relatively an easy matter, the value of intelligent guidance is too obvious to need further mention.

As if to make up for the neglect of past years of the importance—the extraordinary importance—of a fuller knowledge of the beginnings of education and the dawn of intelligence of the young child, there has been of recent years a concentration of investigation on this period by distinguished experts, which has fully compensated for the lack of adequate research in earlier times. The manifest difficulty of discovering by direct observation how the very young child approaches and overcomes obstacles in the great adventure of becoming acquainted with the nature of his strange environment, has to a very considerable extent been aided by experiments with the more intelligent animals.

The great value of this type of investigation is that tasks of varying difficulty can be given to the animals, such as the improvement on repetition, the memory of success in an earlier experiment in attempting a more difficult task of the same nature and so on, can be carried out and conclusions reached. Obviously, it would be impossible to make a young child go through a long series of conditioned experiments, and thus acquire a knowledge which can be obtained so readily by experiments with animals. When isolated experiments of a like nature were carried out with young children, the similarities of response and the means adopted in reaching the desired end were very significant.

The remarkable difference which exists between the child's world and that of the adult presents very serious difficulties in the study of young children. This has, in the past, given rise to much serious misunderstanding as to the real attitude of the child to life. A fertile source of this difficulty is to expect a child to adopt the adult position before the appropriate time in his mental growth has been reached. Long after speech has been acquired, the meaning of a simple expression, in exactly the same words, may convey to the mind of the child something entirely different from the meaning which it conveys to the mind of the adult. Much work in this connexion has been carried on in recent years with considerable success. Many attempts have been made to summarise the main points of difference between the two worlds.

The astounding progress made in the past twenty-five years in our knowledge of the pre-school child must be referred to not only for its intrinsic importance, but also because original work at this stage of development has had such a beneficent effect in popularising education, especially in its social implications. In the school we have a sufficiently large number of children for observation, and possibly for experiment. We can generalise and compare group with group. But the pre-school child is a thing apart, and the nursery is the nearest approach to the class-room. On the physical side the pre-school child is within reach of experts. The local doctor, the mother and the nurse, or other attendant, possess, or should possess, a fair knowledge of childish ailments. On the mental side, however, there is a lamentable deficiency of anything in the nature of expert guidance, the general opinion being that this side of the child's development can safely be neglected until the child goes to school.

We have already pointed out the folly of such

[1] From the presidential address to Section L (Educational Science) of the British Association, entitled "Modern Movements in Education", delivered at Cape Town on July 25.