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A Century of Ideas on Evolution*

By

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INTRODUCTION

For an hour, let us put aside our present anxieties to consider the greatest intellectual adventure in a century of biology: namely, research on evolution. I propose to traverse very briefly the ideas about evolution which were current in 1843; the effect of the publication in 1859 of the *Origin of Species*; the views on evolution held at the time of your Jubilee in 1893; and the 'modern synthesis,' as it has been called in a recent book by Julian Huxley. I am obliged to draw most of my examples from among plants, because I cannot speak from first-hand experience of animals.

1843

The Royal Society of Tasmania was born into a very different world from our own. Lord Shaftesbury was still fighting to prevent children of five being sold as sweeps to climb chimneys, and there was still no legislation to prevent children of ten being employed in factories for as many as 69 hours a week. In 1843 Dickens published *Martin Chuzzlewit* and Carlyle published *Past and Present*. Wagner had begun to write his operas. Huxley was a medical student at Charing Cross Hospital. Darwin, his health broken at the age of 34, had just moved to the country house at Downe, in Kent, where he spent the rest of his life.

It is a mistake to suppose that the ideas of evolution and natural selection originated with Darwin; though it is a worse mistake to suppose that these ideas would have been established without the immense intellectual effort Darwin made. In 1843 biologists as a whole accepted the view that species were immutable, that each new species was the result of a special act of creation. But in the thirty years before 1843 there had been two intellectual crises in natural history, which encouraged speculation and cleared the way for fresh ideas. The first crisis was the realization that fossils were the remains of organisms, and not merely temptations hidden in the earth by Satan. Cuvier and Lamarck in France had compared the skeletons of fossil and living animals and had demonstrated that many creatures of earlier geological ages were unlike living creatures. The second crisis was the acceptance of the principle of uniformity in the geological record. Hutton

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and Lyell, in Britain, had challenged the idea that the past history of the earth was a series of catastrophes; that successive strata of rocks were separated by wholesale extinctions; that each new geological age began with new creations of living things. The old notion of the earth's history as a series of catastrophies died hard. Writing at the coming of age of the *Origin of Species*, Huxley (1907) said that even in 1859 'a scheme of nature which appeared to be modelled on the likeness of a succession of rubbers at whist, at the end of each of which the players upset the table and called for a new pack, did not seem to shock anybody.'

In 1843, therefore, biologists were familiar with the fossil record, and knew that organic remains in the rocks were so different from living forms that they had to be classified as separate species, genera, and families. This did not entail belief in evolution, but it opened the door for the ideas to come in. A member of the Tasmanian Society, Mr. Jukes, wrote in *The Tasmanian Journal* (1846) that the rocks should be looked upon 'as a great series of documents' unfolding 'the wonderful story of the changes which have taken place upon the globe.' Mr. Gunn, of Launceston, communicated an article to the same journal (1846) on the fossil bones of a mastodon, found in Australia. The fossil had been sent to the famous anatomist, Professor Owen. Owen was greatly excited by this evidence of a prehistoric creature closely resembling the mastodons of Europe and America. He wrote to Australia to say 'Depend upon it, your alluvial and newer Tertiary deposits are the grave of many creatures which have not been dreamt of in our philosophy.' This same Mr. Gunn, of Launceston, has put on record in the first volume of *The Tasmanian Journal* (1842) a very interesting comment. He points out that countries whose natural boundaries are formed by mountains, seas, and deserts have floras peculiar to themselves, and yet 'by art' plants may be cultivated outside their natural boundaries of distribution.

It is not surprising that in this atmosphere there were writers who speculated that perhaps the forms of animals and plants were not fixed, but in course of time had changed from one species to another. Lamarck had declared in 1807 that all living species were descended from other species. Dr. Wells had read a paper in 1813 to the Royal Society of London, containing the same suggestion, for Man. In 1822 the Dean of Manchester, the Rev. W. Herbert (see Darwin, 1900) said that 'horticultural experiments have established, beyond the possibility of refutation, that botanical species are only a higher and more permanent form of varieties.' In 1844 Chambers, the Edinburgh publisher, brought out the *Vestiges of Creation* which preached a doctrine of the mutability of species, but it was supported by data so inaccurate that the thesis was condemned in the eyes of all scientific men.

Even natural selection was not a new idea in 1843. Indeed, Dr. Johnson, with characteristic acumen, had thrown it out during a conversation on Easter day, 60 years earlier. Listen to him: 'I believe, Sir' (said Boswell), 'a great many of the children born in London die early, but those who do live are as stout and strong people as any. Dr. Price says they must be naturally strong to get through.'

'That is system, Sir. A great traveller observes that there are no weak or deformed people among the Indians . . . he assigns the reason of this, that the hardship of their life as hunters and fishers does not allow weak or diseased children to grow up. Now, had I been an Indian, I must have died early; my eyes would not have served me to get food.'

All these suggestions, and many others, were no more than ripples upon the sea of scientific opinion. Lamarck's views were dismissed because he went beyond his data. Chambers' views were dismissed because his data were inaccurate. The observations of Wells, Herbert, Grant, and others were too trivial to upset a belief which was taken for granted, and which was consistent with the teaching of the church.

Meanwhile, Charles Darwin was accumulating a more detailed and exact knowledge of natural history than any man before him. 'In October, 1838,' he wrote (1887, vol. i): 'I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence which everywhere goes on from long continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work; but I was so anxious to avoid prejudice that I determined not for some time to write the briefest sketch of it. In June, 1842, I first allowed myself the satisfaction of writing a very brief abstract of my theory in pencil in 35 pages; and this was enlarged during the summer of 1844 into one of 230 pages, which I had fairly copied out and still possess.' This abstract is in outline substantially the book published fifteen years later as the *Origin of Species*. So the year in which Queen Victoria approved the constitution of the Royal Society of Tasmania was the year in which the first draft of the theory of evolution by natural selection was written.

Darwin realized that to drive out belief in the fixity of species would need an immense body of facts. That is why he would not publish his views at once. All his contemporaries: Hooker, Owen, Lyell, the young Huxley, took the fixity of species for granted; indeed, until 1837, Darwin had taken it for granted himself. In a letter written in 1844 or '45 Darwin said (1887, vol. ii): 'In my wildest daydream I never expect more than to be able to show that there are two sides to the question of the immutability of species.' Meanwhile the obvious facts of the fossil record were merely described without being explained. The geologist Lyell wrote (Darwin 1887, vol. iii): 'I taught that as often as certain forms of animals and plants disappeared, for reasons quite intelligible to us, others took their place by virtue of a causation which was beyond our comprehension; it remained for Darwin to accumulate proof that there is no break between the incoming and the outgoing species, that they are the work of evolution and not of special creation.'

Such, in 1843, was the state of opinion about the immutability of species. The idea of evolution through natural selection had been born. Already in the mind of one man there had been a revolution. Sixteen years were to pass before the revolution broke upon the world.

1859

In 1858 a joint paper on evolution by Darwin and Wallace was read at the Linnean Society of London, and in November, 1859, an 'abstract' of Darwin's work was published under the title of the *Origin of Species*. The book was a best seller. The first edition was sold on the day of publication. It took the scientific world by storm: not because the ideas were entirely novel, but because for the first time they were supported by evidence; overwhelming evidence. Darwin, as Huxley said of him, was 'as greedy of cases and precedents as any constitutional lawyer.'

The basis of Darwin's theory can be expressed very simply. He sets out evidence for three facts: (*a*) that populations of organisms multiply in such a way that they should increase geometrically; (*b*) that, in spite of this, the population of any particular species in any region remains approximately constant; (*c*) that organisms belonging to the same species are variable both in structure and function. From the first two facts Darwin deduced that there must be a struggle for survival and a high mortality. From the third fact he deduced that in this struggle there is a selection of the 'fittest' organisms. Variations which confer fitness on the organism will therefore survive and be transmitted to the next generation. For certain parts of his theory Darwin could not secure adequate evidence, and he had to rely on assumptions. These assumptions were: (*a*) that some unknown mechanism caused the appearance of great numbers of small variations in a population; (*b*) that most of these variations are inherited; (*c*) that effects of the environment on an organism are not, as a rule, inherited; (*d*) that a hybrid between two varieties of a species shows a blending of the variations of its parents; (*e*) that despite this continuous blending the variability of a population is sustained. There were several weak points about Darwin's theory, which he noticed himself at the time, and did not attempt to disguise. The first is that on a theory of blending inheritance variation would not be preserved; it would disappear: and this was contrary to observation. The second difficulty was that on the theory of natural selection there would be all gradations between the new species and the old. This, too, was contrary to observation. A third difficulty was that the theory did not explain how, and at what stage, the incompatibility characteristic of many species (i.e., the inability to interbreed) arose in the separation of species. Then there were minor criticisms: how could one distinguish heritable from non-heritable variations? Was the theory consistent with the parable of the sower—was it not a fact that the greater part of mortality in nature was purely fortuitous and did not depend on fitness? How was it that some evolutionary trends, as revealed by the fossil record, seemed to have no adaptive significance at all? To some, Darwin's immense weight of data seemed inadequate to justify a theory so ambitious. His evidence was assembled largely from the experience of plant and animal breeders. The production of new varieties through selection by man was for Darwin a model of the similar, though slower, selection of well adapted types by nature. In his modesty, Darwin was prepared to admit that part of his theory was the substance of things hoped for, the evidence of things not seen.

1893

Darwin's disciples carried the implications of his theory much further than he himself ever intended. As so often happens, admirers were liable to become more embarrassing than opponents. By the time the Royal Society of Tasmania celebrated its Jubilee, in 1893, Darwinism had overcome popular prejudice and religious bigotry, and had won the confidence of almost every biologist. In 1880 Huxley, who had fought for Darwinism when it began as a heresy, had to issue a warning lest it should end as a superstition. And indeed the warning was necessary. Haeckel, in Germany, founded an uncompromising monist philosophy based on Darwin's theory. Arrogant German nationalism found a comfortable justification in the principle of survival of the fittest. Even in the narrower field of biology, Weismann claimed more for the efficacy of natural selection than the data warranted. It looked as though the *Origin of Species* had done for biology what the *Principia* had done for mathematics.

But at the time of your Jubilee, another intellectual revolution had been accomplished in the mind of one man, though it had not yet swept over the world of science. As long before as 1866 Gregor Mendel, afterwards Prälat of the Augustinian Monastery at Brünn, had published in the transactions of the local natural history society two short papers on the mode of inheritance in peas. For 44 years the immense importance of these papers was unrecognized. Suddenly, in 1900, they broke upon the world and shook the very foundations of neo-Darwinism.

The so-called Mendelian laws of inheritance seemed at first to undermine those assumptions that Darwin had to make. Darwin assumed that variation was continuous and that variations blend in inheritance: Mendel proved that variation was particulate, and that the units of variation do not blend in inheritance. Pea plants, for instance, were either tall or dwarf; all other variations in height were due merely to the environment and were not inherited. Moreover, a cross between tall and dwarf was not intermediate in size, but tall. It seemed, therefore, that selection could not work by degrees on minute variations, gradually transforming one variety into another and one species into another through many generations; for the only heritable variations were large. Biologists were in a dilemma: for the fossil record showed evolution to take place by gradual modification through millions of years; whereas this new science of genetics showed that heritable characters were particulate, and it seemed as though modification of species could occur only by big steps. Darwinism declined. In the hands of Bateson in England, Correns in Germany, de Vries in Holland, Mendelism flourished. Fifty years of Darwinism had failed to solve some of the problems of inheritance. Mendelism was solving problems every day. The geneticist succeeded the morphologist in the front line of research. For the time being the problems of evolution were shelved.

We will not pause to follow the fantastic way in which genetics, aided by cytology, brought light into the mysteries of inheritance. We next have to consider how, since the last war, Darwinism has emerged from eclipse. The technique of genetics is now being applied to the study of evolution. The results of this work have been promising beyond the wildest optimism of biologists twenty years ago: I propose to discuss with you some of these results.

A Digression on Genetics

As a preliminary to this, let us digress to review the present state of our knowledge of the laws of inheritance. We know that the units out of which plants and animals are built are cells, and that each cell arises from a pre-existing cell by division. When this division occurs the nucleus undergoes regular changes. It becomes visibly organised into chromosomes. Apart from certain exceptions, these are constant in number and in shape for each species, and it can be recognised that they are in pairs. Each type of chromosome has a similar partner. Thus, in the fruit fly there are four pairs, in the lily 12 pairs, in *Eucalyptus gummifera* 11 pairs, in Man 24 pairs. During cell division every chromosome splits along its length, and every new cell has a complete 'double outfit' of chromosomes. When reproductive cells are about to be formed the chromosomes do not split: instead they assemble in pairs like partners in a dance. One set of chromosomes moves to one side and the partner set to the other side. Thus, in the sperms or eggs of the fruit fly there are not four pairs of chromosomes, but four chromosomes without partners; in the sperms and eggs of Man there are 24 chromosomes without partners; and in the pollen grains and eggs of lily and eucalyptus, 12 and 11 chromosomes without partners. Cells in this condition are said to be haploid. When fertilization occurs the set of chromosomes in the egg is united with a similar set of chromosomes from the sperm or pollen grain. Each chromosome regains a partner. The new organism has a complete double outfit of chromosomes. It is said to be diploid.

These manœuvres of the chromosomes occur, with occasional accidents which I shall mention later, every time reproduction takes place. The chromosomes are, as it were, shuffled and dealt out again in the reproductive cells. It has now been established beyond doubt that almost all the units of inheritance lie on these chromosomes. They are called genes. They determine such characters as eye colour in fruit flies, tallness and dwarfness in tomatoes, right- and left-handedness in Man. In fact, it is possible to draw ‘ chromosome maps ’ which show the position of the genes; and in the salivary glands of some creatures, where the chromosomes are large, it is possible to see, under the microscope, the position of these genes. In the fruit fly, *Drosophila melanogaster*, it is estimated that there are some 5000 genes, and we think their size to be about that of 10 protein molecules, 10^{-8} to 10^{-5} cubic microns (Gulick 1938).

Since the common animal or plant carries a double outfit of chromosomes, it will have two genes for every character. These may be the same or they may be different. If they are different, if, for instance, a fruit fly carries a gene on one chromosome for white eye and a gene on the partner chromosome for red eye, we do not find that the animal strikes a compromise between these two potentialities. It has completely red eyes. In other words, the potentiality for making red eyes masks the potentiality for making white eyes. We say the gene for red eye is dominant and the gene for white eye is recessive. All wild animals and plants carry thousands of recessive genes which do not exert a visible effect on development. But if, as a result of crossing, two recessive genes are brought together, then the recessive character appears. For instance, real albinos, with no pigment in the hair at all, are rare among human beings: approximately one occurs among 10,000 people. There are probably about 25 of them in the whole of Tasmania. But two persons in 100 carry the gene for albinism as a recessive. It may be transmitted as a recessive through generations and it will not be recognised; but if a sperm and an egg, both carrying the gene for albinism, unite, then an albino is born.

These genes are stable over many generations. But occasionally they change suddenly, often with no apparent cause. Thus the genes controlling leaf shape in *Primula sinensis* have changed to produce forms known as maple, tongue, crimp, oak, fern, and many others (fig. 1). These changes are called gene mutations. Once the mutation has occurred it is fixed for good. Mutations are rare: in the fruit fly, for instance, they occur about once in 100,000 individuals.

It used to be thought that every character in the organism was determined solely by its peculiar controlling gene, but we know now that this is an oversimplification. For instance, the recessive gene for crimp leaf, if it is present in two doses, has the major effect on leaf shape, but we think it likely that all the other genes affect shape to some degree. The same mutation for crimp leaf may therefore have a profound effect in one plant, because it is emphasised by the other genes present; in another plant it may have a small effect because it is suppressed by the other genes present: leaves may be ‘ very crimped ’ or ‘ not so crimped.’ This discovery has such an important bearing on the theory of evolution that I want to emphasise it by means of an analogy. Some of you are bridge-players. You know that there is no absolute value to be assigned to, let us say, the knave of hearts. Its effect depends on the other cards in the hand. It might determine the game. It might have no influence at all. The effect of a single card on the outcome of the game is modified by the other cards in the hand. This roughly illustrates our modern views about the effects of genes. Add to the analogy that there are some 5000 to 20,000 cards in the hand, and that from time to time cards 'mutate' into entirely new cards never seen before and which you are allowed to play, and you have some inkling of the possibilities of Mendelian inheritance.

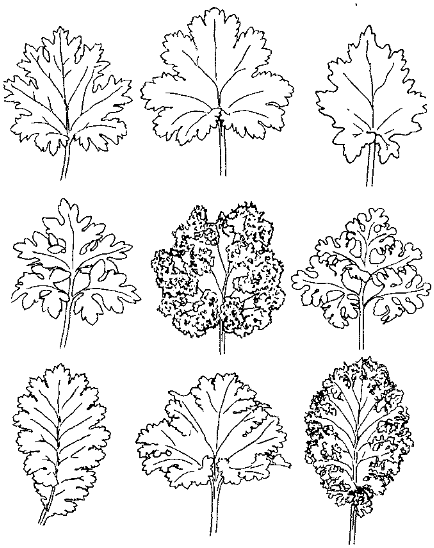

FIG. 1.—Leaves of *Primula sinensis* showing effects of single genes on shape. (after de Winton and Haldane.)

Here, then, is the first missing piece of evidence for Darwin's theory. Darwin made no suggestions about the causes of variation: he confined his discussion to the consequences of variation. We now know that variation is due to recombinations of genes following crossing, and that variation among genes is due to occasional gene mutations. At first it seemed as though this evidence was inconsistent with Darwinism, because it led to the conclusion that evolution is essentially discontinuous. The 'all-or-none' reaction to genes by the organism led to the assumption that species differences, which depend on genes, should be sharp and unmistakeable; and this assumption was inconsistent with the fossil record. This apparent inconsistency contributed to the eclipse of Darwinism: but it has been resolved by recent research. For we now know that the effect of a mutation is buffered by all the other genes present, and we may therefore expect to find under some circumstances a graduation of types from mutant to normal.

The second important piece of evidence missing from Darwin's data was the machinery for producing infertility. How could a population of one species become split into two or more species which are infertile with each other? Almost invariably the genetical types within a species will interbreed. White sweet peas cross with red sweet peas: black cats cross with tabby cats; tall tomatoes cross with dwarf tomatoes. Commonly (although not invariably) distinct species will not interbreed. How, then, can species arise from genetical types? The first evidence from genetics seemed to contradict Darwin's assumption that sterility would follow the origin of new species. This was another reason for the eclipse of Darwinism; but recent research has resolved this apparent disagreement too. For we now know that some gene mutations confer sterility in cross breeding; and that there are other sorts of mutations beside gene mutations: other sorts of accidents to the chromosomes which confer sterility. For instance, there is sometimes a breakdown in the mechanism which 'deals out' chromosomes in cell division. This results in the formation of cells with four times, six times, eight times the basic number of chromosomes. When this occurs in animals the cells die and the results of the accident are not carried into the next generation. But if it occurs in plants it gives rise to what we call polyploids. Often these polyploids have all the appearance of new species. They are fertile with one another and they are usually infertile with the plants from which they arose. It is now established that a very great number, perhaps the majority, of present-day species of plants are polyploids, with 4, 6, 8, 12 . . . complete outfits of chromosomes, or with irregular numbers of extra chromosomes. For instance, the various species of Chrysanthemums have 9, 18, 27, 36, or 45 chromosomes. The wild strawberry, *Fragaria vesca*, has 14 chromosomes; *Fragaria elatior*, the cultivated strawberry of the sixteenth century, has 42 chromosomes; the modern garden strawberry has 56 chromosomes. Dahlias have 16, 32, or 64 chromosomes, according to the species.

Choromosome accidents can take the form also of the breaking off of parts of chromosomes and their joining up to other chromosomes; or their breaking off and rejoining upside down: these are so-called translocations and inversions. At first sight translocations and inversions would seem to have little effect on the organism because the same genes are there: only their order on the chromosomes has been changed. But there is, in fact, a 'position' effect of genes. Their influence on development does depend on their place in the chromosome outfit: a phenomenon which has no analogy in a hand of cards! Furthermore, if chromosomes have been broken and rejoined in a fresh position they frequently will not pair with ordinary chromosomes on fertilization. Therefore, the new race with translocations and inversions is not fertile with the old race from which it has come. Those are two ways in which sterility between species can arise; so that we have, to-day, evidence which dispels another of the difficulties in the way of accepting Darwin's theory. It is on account of these discoveries, and others like them, that Darwinism is now reinstated and interest in evolution through natural selection is revived.

Genetics has made another, and quite different, contribution to the study of evolution. You are familiar with the way anatomists and morphologists have sought over the last century for evidence of relationship between similar types of animals: comparative anatomy has been the taking of evidence for evolution. The study of comparative genetics has confirmed the results of anatomy and morphology. By studying the genes present in related forms we obtain strongly presumptive evidence of their common ancestry. For instance, tables have been prepared (table I) which show the genes known for coat colour in rodents (Haldane quoted by Waddington, 1939). There is a similar table (table II) for genes in four species of cotton (Harland, 1936).

TABLE I

Gene	Effect	Mouse	Norway Rat	Black Rat	Deer-mouse	Cavy	Rabbit
C	Normal	+	+	+	+	+	+
c^k	Slight dilution	—	—	—	—	D	+
c^d	Marked dilution	—	—	—	—	D	+
c^r	No yellow	D	D	—	—	D	D
c^b	Himalayan	D	—	—	—	D	D
c^a	Albino	D	D	—	D	—	D
A^y	Yellow	D	—	—	—	—	—
A^w	Light bellied grey	W	+	+	+	—	+
A^g	Grey bellied grey	+	—	W	—	+	—
A^r	Ticked bellied grey	—	—	—	—	W	—
a^t	Black and tan	—	—	—	—	—	D
a	Black	D	D	D	—	D	D
E^d	Black	—	—	D	—	—	D
E^s	Black	—	—	—	—	—	D
E	Normal	+	+	+	+	+	+
e^p	Bicoloured	—	—	—	—	D	D
e	Yellow	? D	—	D	D	D	D

TABLE I.—Some homologous genes in rodents. A 'plus' indicates that the gene occurs in the normal type; 'W' that it is found in the wild races; 'D' that it is found in domesticated animals. (after Haldane.)

TABLE II

Gene	Effect	*purpurascens*	*taitense*	*tomentosum*	*Darwinii*
R^H	Red plant body	n.r.	n.r.	n.r.	n.r.
r^H	Green plant body	p.f.	p.f.	p.f.	p.f.
R^B	Red plant body	Common in West Indies form	n.r.	n.r.	n.r.
r^B	Green plant body	p.f.	p.f.	p.f.	p.f.
R^D	Red plant body	n.r.	n.r.	n.r.	Found in one type, prevalence not known
r^D	Green plant body	p.f.	p.f.	p.f.	p.f.
Y^B	Yellow corolla	Character present but probably due to another allele	n.r.	Character present but probably due to another allele	n.r.
y^B	Cream corolla	Rare	p.f.	n.r.	n.r.
Y^D	Yellow corolla	n.r.	n.r.	n.r.	p.f.
y^D	Cream corolla	Rare	p.f.	n.r.	n.r.
S^B	Petal spot	Allele present but not known whether identical with S^B or S^H	Apparently represented by another weaker allele	n.r.	Allele present, probably different from S^B or S^H
S^H	Petal spot			n.r.	
s	No petal spot	Rare	n.r.	p.f.	n.r.
P	Yellow pollen	p.f.	n.r.	p.f.	p.f.
p	Cream pollen	Rare	p.f.	n.r.	n.r.
O^N	*hirsutum* leafshape	Allele present, not certain if identical	Allele present, not certain if identical	Allele present, not certain if identical	Allele present, not certain if identical
O^O	Upland okra	Occurs rarely	n.r.	n.r.	n.r.?
O^S	Upland super-okra	n.r.	n.r.	n.r.	n.r.
O^P	Laciniated leaf *purpurascens*	Rare	n.r.	n.r.	n.r.
O^D	Laciniated leaf *Darwinii*	n.r.	n.r.	n.r.	Occurs
O^B	Sea Island leafshape	n.r.	n.r.	n.r.	n.r.
C^{ha}	Green	p.f.	n.r.	p.f.	p.f.
c^{ha}	Chlorophyll deficient	Rare	p.f.	n.r.	n.r.
C^{hb}	Green	p.f.	p.f.	p.f.	n.r.
c^{hb}	Chlorophyll deficient	n.r.	n.r.	n.r.	p.f.
C^o	Contorta leaf	n.r.	n.r.	n.r.	n.r.
c^o	Normal leaf	p.f.	p.f.	p.f.	p.f.
C^R	Normal	Allele present	Allele present	Allele present	Allele present
c^R	Crinkled leaf	n.r.	n.r.	n.r.	n.r.
K^B	Khaki lint	?	n.r.	n.r.	?
K^H	Khaki lint	?	Found	n.r.	?
K^T	Khaki lint	n.r.	n.r.	p.f.	?
k	White or cream lint	p.f.	n.r.	n.r.	n.r.
G^L	Green lint	—	—	—	—
g^L	White or cream lint	p.f.	p.f.	p.f.	p.f.
V	Green leaf	p.f.	p.f.	p.f.	p.f.
v	Virescent yellow leaf	n.r.	n.r.	n.r.	n.r.
H^T	Hairy plant body	n.r.	n.r.	p.f.	?
h^T	Glabrous plant body	p.f.	p.f.	n.r.	?
H^B	Hairy plant body	n.r.	n.r.	n.r.	?
h^B	Glabrous plant body	p.f.	p.f.	p.f.	?

Note. n.r. (not recorded) indicates that the gene was not present in all types of the species which it was possible to examine. p.f., prevailing form.

TABLE II.—The distribution of genes in four species of Gossypium. (after Harland.)

The advances made in genetics since the Jubilee of your Society have entirely changed our outlook on the mechanism of evolution. Since 1893 the fact of evolution has remained unquestioned by scientific men. Ideas as to the mechanism of evolution have passed through three phases: at first a sturdy belief in natural selection as the sole driving force; then a period of disillusionment and a discrediting of natural selection; then a period of experimental work which has illuminated the theory of natural selection. To-day, at your Centenary, we can admire a splendid building on the foundations Darwin laid. The working of natural selection has been demonstrated. The consequences of it have been worked out mathematically. The origin of variations and the causes of sterility between species have been explored.

So let us return from this digression to see where Darwinism stands to-day. I shall occupy the rest of this lecture with a summary of modern views on the origin of species. The fact that evolution has occurred we may take for granted. Lyell, Darwin, Huxley, Wallace established this beyond further discussion. We now have actual pedigrees of fossil types: horses, elephants, camels, sea urchins, ammonites, pines. Let us proceed at once to discuss first, the evidence for natural selection, and, second, the mechanisms whereby new species are formed.

1943

The Evidence for Natural Selection

Robson and Richards published in 1936 a book entitled *The Variation of Animals in Nature*. In it they examine critically the numerous examples of alleged natural selection among animals. They come to the conclusion that, even to-day, the hypothesis of natural selection is not supported by adequate data, and judgment upon it must be suspended. This conclusion is, I think, unjustifiably pessimistic; but it is interesting that, even a century after the first draft of Darwin's essay, the evidence that species originate through natural selection should still be so scrappy, and to some even unconvincing.

In my opinion there is a good deal of evidence that natural selection does operate to favour the transmission, from one generation to the next, of some genes in preference to others. I propose to describe two examples. The first is a Russian experiment by Sapegin (quoted by Haldane, 1932) to discover the fate of a mixed batch of wheat grains, harvested and sown on the same plot in successive years. In 1913 a mixture of five varieties of wheat was sown in the proportions shown in the following table (figures in percentages). The columns under 1915 and 1917 show the composition of the population in those years:—

Variety.	1913.	1915.	1917.
Durum and compactum	2·5	0	0
Milturum	5·5	9	5
Lutescens	72	31	6·5
Erythrospermum	10	19	5·5
Ferrugineum	10	41	83

There is no escape from the conclusion that in this plot the variety ferrugineum flourished at the expense of the other varieties, one of which was eliminated completely.

A second example concerns what is known as 'industrial melanism' in moths (Huxley, 1942). The moth *Boarmia repandata* is normally grey, but it has a mutation to a dark (melanic) form which is dominant to the normal form. Under some conditions the melanic forms even show a higher viability, and so they are 'fitter' in Darwin's sense of the word. In country districts the percentage of melanics remains low. In industrial districts, on the other hand, the percentage is high. This difference between town and country moths is not correlated with any difference in diet or climate, and can most easily be attributed to selection.

In the country the dark colour is conspicuous and lowers the chance of survival; in the industrial town it increases the chance of survival.

The experimental study of natural selection is complicated by the multiple effects of genes and by what we might call the capricious policy of nature as a selector. Let me enlarge on these two circumstances. A gene is usually named by some visible effect, but it may exert physiological effects far more important for the survival of the organism. For instance, mutations called 'arc' wing and 'speck' on the axilla of *Drosophila* also lower the average number of progeny hatched during a lifetime; and the mutation called 'purple' eye increases the number of progeny. An experiment by Gordon (1935) demonstrates how selection occurs in nature against an apparently harmless mutation. Gordon released 36,000 individuals of the fruit fly *Drosophila melanogaster* in a Devon orchard. *Drosophila* does not occur wild in England, so the population was quite isolated. The population consisted of 25 per cent normal flies, 25 per cent pure 'ebony' flies, and 50 per cent of flies heterozygous for ebony (i.e., carrying one recessive dose of ebony). After 120 days, when there had been five to six generations of flies, Gordon trapped samples to determine the proportion of 'ebony' in the population. He found that the frequency of the ebony gene had fallen from 50 per cent at the beginning to 11 per cent. This indicates that there must be some physiological 'unfitness' correlated with ebony colour.

The second complication is the capriciousness of nature as a selective agency. The organism is subjected, as it were, to an examination by nature for which there is no syllabus. It is therefore impossible to predict whether this or that variation may prove to be useful. I have already given you one example of this, namely, 'industrial' melanism in moths. Here are two more. There is a mutation in *Drosophila* called 'vestigial wing.' The name is self explanatory. Under ordinary conditions vestigial winged flies have a lower expectation of life than normal flies. But under conditions of starvation, or in a high wind, vestigial-winged flies live longer than normal flies. The 'policy' of natural selection is reversed (Huxley, 1942). A similar instance is cited by Engledow for wheats (1925). He compared yields from two wheats (Red Fife and Hybrid H) sown at three different distances apart. When the wheats were spaced at 2″ by 2″ Red Fife gave the greater yield. When they were spaced 2″ by 6″ the yields from the two varieties were equal. At wider spacing still, Hybrid H gave the greater yield. The trend of natural selection will, therefore, depend on the spacing between the plants.

Sometimes the capriciousness of selection leads to quite fantastic results. For instance, Vavilov has recorded the occurrence of mimicry in seeds as striking as any known among insects. In parts of India lentils are grown by the peasants. There is no standardization or distribution of seed. Each peasant keeps a batch of seed from his harvest to sow in the following season. Consequently the samples of lentil seed from different districts vary in colour and size. Before planting his seed, the peasant picks it over to remove weed seeds. Seeds easily distinguished from lentils are easily removed, but any seeds resembling lentils are hard to distinguish and would not be removed. It so happens that one of the weeds, a species of *Vicia,* has seeds not unlike lentil seeds. Now any variation in the vetch seed which makes it more closely resemble a lentil seed will tend to be preserved, because the peasant will not notice it as he sorts out his seed. Accordingly, it has come to pass that the vetch weed seed in each district closely mimics the lentil seed grown in that district; so closely that it is very difficult to distinguish the two. Another example is quoted by Salisbury (1929). The fools parsley (*Aethusa cynapium*) has dwarf strains which inhabit wheat fields.

Taller strains which appear each year are decapitated by the reaper, and so do not flower. The dwarf strains can flower in the stubble. This may be the first stage of the production of a new species, for not only genes for dwarfness, but other genes (e.g., those controlling late flowering), will be selected in this environment.

These examples, even those which illustrate the complexity of selection, are sufficient to demonstrate that the passage of genes from one generation to the next is influenced by selection. The examples do not, of course, prove that new species arise as a result of this process; but if it is established that species differences are due to gene differences, we have evidence of the part played by gene selection in the origin of species. For some hundreds of species this fact has been established. It is known, for instance, that the different species of *Phaseolus* (the bean), *Gossypium* (cotton), and *Antirrhinium* are due to gene mutations. So also are the varieties and species of the snail *Partula*.

The amount of selective advantage which a mutant gene needs in order to establish itself is very small. Fisher (1930) and Haldane (1932) have worked out that a mutation occurring only once in 100,000 individuals, and with a selective advantage of only 1 per cent (i.e., a 1 per cent higher chance of surviving to the next generation) will spread through half the population in 100 generations: that is, for *Drosophila*, in 7 to 8 years; for a wallflower, in a century; for Man, in about 3000 years.

We may not dwell longer on this subject. Since Darwin's time our ideas of the operation of natural selection have changed in one important respect. There have been two steps in the change. Darwin supposed that variations, whose origin he did not specify, were directly selected by nature. Organisms with 'fit' variations survived. The rest perished. The first step in advance of this was the discovery that Darwin's variations are due to gene mutations. It was then supposed that the mutation appeared in the race and natural selection either favoured its survival or eliminated it as unfit. To-day we have gone a step farther. We now suppose that the effect of a mutation is buffered by the rest of the outfit of genes in the organism. Natural selection does not work to preserve or eliminate single genes. Selection modifies the reaction of the whole gene outfit. If a mutation is favourable, then organisms which exaggerate it are favoured in the struggle for survival. If a mutation is harmful, then organisms which suppress it are favoured. In the terms of our analogy of cards, it is the whole hand, not the single card, which determines the game.

The verdict of 1943 is, therefore, broadly in favour of Darwin's theory. But we know, to-day, that natural selection is not the sole *deus ex machina* of evolution. In fact, no single generalization can be made about the origin of new types of organisms. All we know of the evolution of the horse is irrelevant for a study of the evolution of wheat. Our knowledge of the evolution of evening primroses throws no light on the evolution of eucalypts. In brief, as Julian Huxley has put it (1942), if Darwin had to write his book to-day he would call it the *Origins of Species*. Sometimes natural selection plays a part in these origins: sometimes it does not.

From our knowledge of genetics we are satisfied that so long as free interbreeding continues between the individuals in a population, the genes responsible for variation will be distributed through that population; there will be no splitting into fresh types which breed true. It may appear that there are fresh types, but they are only so-called ecotypes. Let me illustrate what I mean by an example. Gregor (1939) found that plants of the sea plantain (*Plantago* *maritima*) on coastal mud flats look quite different from plants on rocks. But the two types interbreed freely, and these two kinds of environments select anew every year the most appropriate outfits of genes. There is no good evidence that the sea plantain will break up into new species this way, unless the mud flat type becomes isolated from the rock type, and will no longer interbreed with it.

This brings us to the core of the problem. The machinery of evolution depends on the ways in which communities become isolated. For we know that once a community is isolated, gene mutations will accumulate in it; other chromosome accidents such as polyploidy, inversion, and translocation may occur. All these cause variations on which local influences of selection may work. And the result will be new varieties, ultimately new species. In a small community, where interbreeding is limited, or where competition is not severe, not only useful adaptations but all sorts of 'useless' characters may survive in the community. Isolation is the prerequisite of evolution. Isolation alone can lead to the origin of species. Let us, therefore, review the ways in which isolation may occur.

There are four kinds of isolation, all of which prevent interbreeding and each of which gives rise to its own peculiar type of species. The four kinds are:

Isolation in time, giving rise to geological species.
Isolation in space, giving rise to geographical species.
Isolation in function, giving rise to ecological species.
Isolation in genetic mechanism, giving rise to genetic species.

Geological Species

The most extreme isolation is that which separates species of one geological age from those in another. It is possible that some fossil types, if they were still alive, might interbreed with living types. Some of the divergence between fossil and living forms is, therefore, due to their isolation in time. We have some inkling of the genetic basis of fossil characters from occasional mutations in living types. For instance, the ancestors of guinea pigs undoubtedly had five toes to their limbs. Living guinea pigs have four toes on the front feet and three on the hind feet. But Sewall Wright in Chicago (1935, fig. 2) has studied a mutation in guinea pigs which, as a heterozygote (one dose of the mutant) gives five-toed animals.

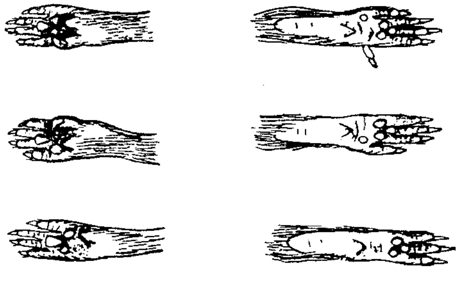

FIG. 2.—Forefeet and hind feet of normal and heterozygous guinea pigs. (after Wright.)

The most remarkable circumstance about evidence from fossils is the presence of consistent evolutionary trends. These are still among the unsolved problems of evolution, and they have given rise to a crop of philosophical theories: emergent evolution, orthogenesis, élan vital and the like. Unfortunately, there is no time to refer to them in this lecture.

Geographical Species

Let us now consider the origin of geographical species. Since the time of Lamarck it has been recognised that geographical isolation produces new species. The flora and fauna of Australia are among the striking examples of the effects of isolation. It is now pretty clear that geographical isolation alone, even without natural selection, will lead to a diversity of animals and plants. Even though the same mutation occurred in separated communities of the same species, the results would be different, for the effects of the mutation depend on the other genes present.

There are good examples of geographical species among your own eucalypts. Out of twenty-two species of *Eucalyptus* in Tasmania, ten are endemic. This is clearly not due to the endemics having a narrow climatic preference, because some of them (e.g., *Eucalyptus globulus*) are widespread under cultivation in other States.

Geographical isolation is often due to less obvious barriers than seas and mountains. The range of migration is sometimes determined by cities or by cultivated land. The distribution of the tropical fruit fly, *Drosophila hydei* is an example of this. In the U.S.A. this fly occurs only on decaying fruit, on refuse heaps and such like. It passes the winter, in greatly reduced numbers, in fruit stores, restaurants, and cellars. In the summer it multiplies and spreads in the open. But it is always a hanger-on of human communities, and there is almost complete geographical isolation between the *Drosophila* populations of different towns. Recently Spencer (1941) has compared the appearance and gene outfits of two populations: one on a refuse heap in Azusa, California, and the other in Wooster, Ohio. He examined 50,000 flies. He found that the mutations accumulated in the Ohio population were quite different from those accumulated in the Arizona population, so that one might say that here are already two geographical races, differing genetically. If these two races were mixed, any divergence between them would vanish. If they remain in isolation, and chromosome accidents accumulate in them, they may become two different species.

Ecological Species

The third kind of species-forming process is ecological. Without any geographical barriers, local differences in habitat or in behaviour may isolate animal and plant communities. This will produce in the isolated community a pocket of diversity, as it were, from which new species may emerge. Tasmanian eucalypts, which, as a group, illustrate the effects of geographical isolation, provide among themselves examples of ecological isolation. Thus, the Mt. Wellington peppermint, *E. coccifera,* is separated from the giant gum, *E. regnans*, because the two species prefer different environments. It may be that they hybridize and the hybrids may be eliminated by natural selection. Or it may be that they cannot interbreed because they flower at different times, or because they are incompatible. That remains to be discovered. The exact cause of isolation is not known, therefore: it is unlikely to be geographic; it is unlikely that pollen from one does not reach ovules of the other; it may be functional; it may be genetical.

Very slight functional differences may isolate communities and so set them on the road to diversification. Differences in season of flowering; differences in the time of day flowers open; differences in flower colour which determine the kinds of visiting insects: any of these may isolate a plant community. In the same way Dobzhansky (1937) reports that species of certain butterflies in California are isolated from each other owing to differences in the time at which the adults emerge. For instance, *Philotes sonorensis* flies from February to April and *Philotes battoides bernadino* flies in May.

It is, of course, impossible to classify many species or varieties as geographical or ecological: frequently both these kinds of isolation play a part in making a species. Among the variations whose cause cannot be assigned is the distribution of the black brush opossum in Tasmania. The story is familiar to you, for it was worked out by Dr. Pearson (1938) and published in your papers for 1937. Dr. Pearson summarized the distribution of black and grey opossums as phenocontours on a map. The black pigment is, doubtless, due to a gene mutation, possibly with modifiers (i.e., other gene mutations). It is likely that the mutation arose in Tasmania, because there are no black opossums on the mainland. The proportion of blacks falls toward the south and east, and is lower on Tasman Peninsula than on the adjoining coast. The distribution might be due to several causes, e.g., (*a*) incomplete geographical isolation within Tasmania, due to a limited range of wandering of the opossum. On this hypothesis the island was originally populated by grey opossums. A black mutation arose in the N.W. and has spread slowly along the paths of migration. This would imply that the black form had some 'additional' fitness which is selected irrespective of environment; and the proportion of black opossums in any locality would measure the time the black gene has existed in that locality; (*b*) a second cause of the distribution might be incomplete ecological isolation. On this hypothesis the distribution of the black form would depend on its having some adaptive advantage in parts of Tasmania. If this were so the proportion of black opossums in any locality would measure the selective advantage of black for that locality.

Dr. Pearson states that there is no correlation between the distribution of black forms and elevation or rainfall; though there is some evidence that for other animals melanic forms are commoner in damp, cool climates: Huxley (1942) quotes the work of Timofeeff-Ressovsky on hamsters (*Cricetus cricetus*) in support of this. I have quoted this example, however, not to try to explain it, but to illustrate the type of diversity which cannot, with confidence, be put into either of the last two categories of species.

Genetic Species

Lastly, let us review the modes of formation of genetic species. It is clear that the integrity of geographical or ecological species depends (when they first appear, at any rate) on the maintenance of geographical or ecological isolation. If the mountain barriers are overcome, if the seas are crossed, then interbreeding takes place and the species dissolve. In New Zealand, and probably to a greater extent than we realise in this country, there are among plants hybrid swarms of species. Mr. Brett has recorded excellent examples from among Tasmanian eucalypts. They are the despair of the taxonomist because they are not isolated in their breeding. But if geographical or ecological isolation lasts long enough, then changes will occur in chromosome outfits which will lead to incompatibility. Until differences in the genetic mechanism between races make interbreeding impossible, or very difficult, there is no sure stability of species.

I have already mentioned how certain mutations or accidents to the chromosomes—polyploids, inversion, translocation, and certain gene mutations, lead to incompatability. When this happens the mutants may be growing alongside the community from which they came, but they are as effectively isolated as though an ocean lay between. The researches of the last 25 years have brought to light hundreds of examples of species determined by genetic isolation. For instance, the essential difference between two species of oats (*Avena sativa* and *Avena fatua*) depends on an inversion of one chromosome which makes interbreeding very hard. The difference between *Drosophila pseudo-obscura* and *Drosophila miranda* depends upon the simultaneous presence of three sorts of chromosome changes: new and different genes, translocations, and inversions (fig. 3). Otherwise there is a similarity in the chromosomes (of number, shape, size, and gene arrangement) which is itself strong presumptive evidence that the two species originated from one another, or from a common ancestor (Waddington, 1939). A recent study by Lamprecht (1941) of the difference between *Phaseolus vulgaris* and *P. multiflorus* leads to the conclusion that the cause of species formation is gene mutation. Some of the mutations have lowered the ability of the two species to interbreed. The most striking gene-controlled differences are:

	Phaseolus vulgaris.	*P. multiflorus.*
Inflorescence at:	2-5th node	10-16th node
flower colour	no genes for red	genes for red
pods	not grooved	grooved
hilum of seed	colour not localized	colour localized

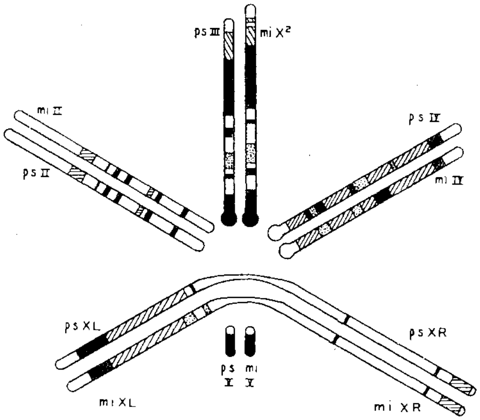

FIG. 3.—Comparative chromosome maps of *Drosophila pseudo-obscura* and *D. miranda.* Regions with the same gene arrangements are white; inverted sections, cross hatched; translocations, stippled; and sections of which homologues are not detectable in the other species, black. (Waddington from Dobzhansky.)

Another common cause of genetic isolation in flowering plants is polyploidy: the presence of 3, 4, 6 or more complete chromosome outfits. For instance, the various species of wheat fall into three groups: the so-called *Einkorn* group with 14 chromosomes (a double outfit of 7); the *Emmer* group with 28 chromosomes (a quadruple outfit of 7); and the *Vulgare* group with 42 chromosomes (six outfits of 7). There is evidence that emmer-type and vulgare-type wheats have arisen from einkorn-type wheats, but they are sterile when crossed with einkorn wheats. When emmer and vulgare wheats are crossed, some fertile offspring are obtained: this proves their 'blood-relationship,' though the chromosomes behave irregularly.

We have abundant evidence that new species arise in nature through polyploidy. Perhaps the most striking example is the origin of rice grass, *Spartina townsendii* (Huskins, 1931). Up to a few years ago two species of *Spartina* were found on the Southern Coasts of England: *S. stricta,* a native of Britain, and *S. alternifolia,* imported from America. A few years ago a new species appeared. It was named *Spartina townsendii.* It was undoubtedly a new species, and it was more vigorous than the other two species: so much so that it was soon being used by the Dutch for reclaiming land from the sea. A study of the chromosome numbers showed that *Spartina stricta* has 56, *S. alternifolia* has 70, and *S. townsendii* has 126. *Townsendii* is a polyploid from a combination of *alternifolia* and *stricta.* It breeds true and will not cross with its ancestral types because polyploidy confers a high degree of incompatibility. The hemp nettle, *Galeopsis tetrahit* has arisen in the same sort of way from two diploids, *G. pubescens* with 16 chromosomes and *G. speciosa* with 16 chromosomes: and in 1932 Müntzing (1932) succeeded in crossing *G. pubescens* and *G. speciosa* and producing a 'synthetic' hybrid, exactly like *G. tetrahit.*

These are examples of genetic isolation. It is evident that species can arise without geographical isolation. It is enough for there to be a gene mutation which makes the individual unable to breed with the rest of the race. By polyploidy, or by the breaking up and rejoining of chromosomes during cell division, races can be formed which may live alongside the rest of the species and yet be isolated from it. Once the race has been isolated, then it will run its own course of evolution; it will change and be diversified by mutations, untouched by the main group from which it has become detached. Thus it is possible for races to diverge, and to evolve into new species, without natural selection. There may be no difference in fitness between the new race and the mother community. That will not matter. Mutations will continue to arise in the new race, and especially in small populations, selection will be weak. Under these conditions there can certainly be an origin of species without geographical or ecological isolation, and not dependent on natural selection.

But selection is ever waiting, as it were, to work on differences in fitness, and we have some interesting evidence that polyploids in general are fitter than the diploids from which they come. For instance, almost all grasses at Spitzbergen are, according to Haldane, polyploids. Other polyploid grasses are common in deserts (Hagerup, 1932). On theoretical grounds, too, polyploids should be 'fitter,' because when there are four or six outfits of chromosomes instead of two there is less chance of harmful genes weakening the race: there is more chance that they are masked by the dominant genes in other chromosomes.

Finally, I shall mention one example of the historical evidence for evolution by polyploids. There is a European crucifer, *Biscutella laevigata,* which occurs in both diploid and tetraploid forms. Manton (1934), has shown how the diploid forms are confined to valleys not covered by ice at the last glacial period. The tetraploid forms occupy stretches of Europe once covered by ice. It appears that the diploid *Biscutella* is a vestige of the flora of Europe before the Ice Age, and the tetraploid *Biscutella* has succeeded it except in a few areas (fig. 4).

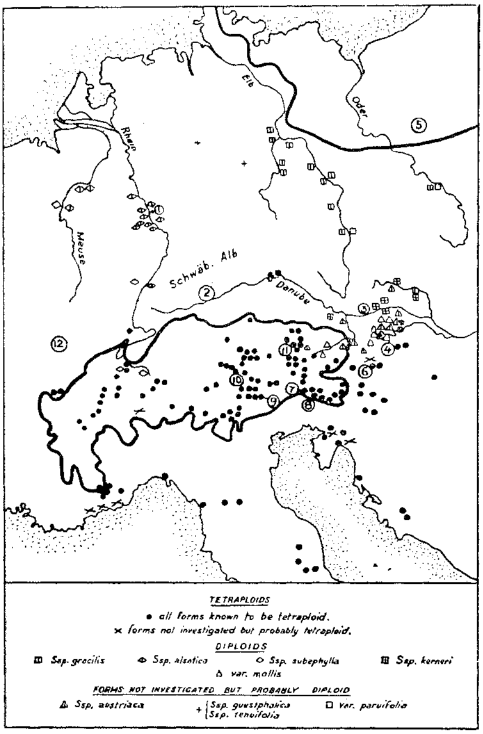

FIG. 4.—Distribution of diploid and tetraploid species of *Biscutella* in Europe. (after Manton.)

It is time to sum up. The centenary of this Society falls at a time when interest in evolution has revived, at a time when evolution is being studied more vigorously than ever before. Many of the blank spaces in the map of evidence Darwin relied upon have been filled in. We ought to know our way about nature better than he, for we have far more powerful instruments for exploration. We have fuller confirmation than Darwin had of the fact that evolution has occurred. We have more evidence of the working of natural selection to produce new forms. For Darwin's assumption of inheritance by blending we can substitute the beautiful, clear mechanisms revealed by genetics. For Darwin's confession that he did not know the causes of variation we can substitute our knowledge of gene mutation; of inversion, translocation, polyploidy, and the reaction of the whole outfit of genes to a change in any one of them. Where Darwin relied on observation we can use the sharper instrument of experiment. Where Darwin imagined one origin of species, we recognise several origins of species: where he assumed one process of evolution, we assume many processes. Yet Darwinism is not out of date. In the study of evolution the scientific victories of the 1940's depend on the master strategy laid down in the 1840's.

One more point: the last. In the study of evolution much has been accomplished, but much remains to be done. We know a good deal about the origins of species, but we still have no adequate hypothesis to explain the grand sweep of evolution. With all our experience we cannot account for the evolutionary trends in such groups as the ferns or gymnosperms, ammonites or spirifers. This is only one example of our ignorance. In fact, it would not be difficult to give another lecture on the unsolved problems of evolution: problems about which we are as ignorant to-day as our predecessors were in 1843.

It is gratifying to recall that Tasmania has the honour of a rare compliment from Darwin, and that the City of Hobart played a part in the first stage of the intellectual adventure I have described to-night. Over and over again Darwin acknowledged his debt to Sir Joseph Hooker, and he drew some of his evidence from Hooker's work. In 1854 the Tasmanian Government made an unsolicited grant of money towards the cost of publishing Hooker's Flora of Tasmania. Hooker wrote to Darwin to tell him of this. Here is Darwin's reply (Darwin, 1887, vol. i):

> 'What capital news from Tasmania: it really is a very remarkable and creditable fact to the colony. I am always building veritable castles in the air about emigrating, and Tasmania has been my headquarters of late: it is really a very singular and delightful fact, contrasted with the slight appreciation of science in the old country.'

It has been a pleasure to discuss Darwin's work in a city which earned this high compliment from him.

LITERATURE CITED

DARWIN, C., 1900.—*The Origin of Species*, 6th Edition. Historical Sketch.

DARWIN, F., 1887.—*Life and Letters of Charles Darwin.* 3 Vols.

DOBZHANSKY, T., 1937.—*Genetics and the Origin of Species*, p. 235.

ENGLEDOW, F. M., 1925.—Investigation on Yield in the Cereals. *Journ. Agric. Science*, Vol. XV, p. 124.

FISHER, R. A., 1930.—*Genetical basis of Natural Selection.* Oxford.

GORDON, C., 1935.—Experiment on a released population of *D. melanogaster*. *Amer. Nat.*, Vol. LXIX, p. 381.

GREGOR, J. W., 1939.—Experimental Taxonomy, IV. *New Phyt.*, XXXVIII, p. 293.

GULICK, A., 1938.—What are the Genes? *Quart. Rev. Biol.*, Vol. 13, p. 140.

GUNN, R. C., 1846.—Communicating a letter from E. C. Hobson on fossil bones from Mount Macedon. *Tas. Journ.*, Vol. II, p. 344.

GUNN, T. C., 1842.—Observations on the flora of Geelong. *Tas. Journ.*, Vol. I. p. 203.

HAGERUP, O., 1932.—Über Polyploidie in Beziehung zu Klima, Ökologie u. Phylogenie. *Heriditas*, XVI, p. 19.

HALDANE, J. B. S., 1932.—*The Causes of Evolution.* London.

HARLAND, S. C., 1936.—The Genetical Conception of the species. *Biol. Rev.*, Vol. XI, p. 83.

HUSKINS, C. L., 1931.—The origin of *Spartina townsendii*. *Genetica*. Vol. XII, p. 531.

HUXLEY, J., 1942.—*Evolution: The Modern Synthesis.* London.

HUXLEY, T. H., 1907.—The Coming of Age of the Origin of Species. *Collected Essays.* Vol. II.

JUKES, J. B., 1846.—A few remarks on the nomenclature and classification of rock formations. *Tas. Journ.*, Vol. II, p. 1.

LAMPRECHT, H., 1941.—The Limit between *Phaseolus vulgaris* and *P. multiflorus*. *Proc. VII, Int. Cong. Genetics*, p. 179.

MANTON, I., 1934.—The problems of *Biscutella laevigata* Z.I.A.V., LXVII. p. 41.

MUNTZING, A., 1932.—Cytogenetic investigations on synthetic *Galeopsis tetrahit*. *Hereditas*, XVI, p. 105.

PEARSON, J., 1938.—The Tasmanian Black Brush Opossum. *Papers & Proc. Roy. Soc. Tas.*, 1937, p. 21.

REUSCH, B., 1939.—Typen der Artbildung. *Biol. Rev.*, XIV, p. 180.

ROBSON, G. C. and RICHARDS, O. W., 1936.—*The Variation of Animals in Nature*. London.

SALISBURY, L. J., 1929.—The biological equipment of species in relation to competition. *Jour. Ecol.*, XVII, p. 197.

SPENCER, W. P., 1941.—Ecological factors and the distribution of genes in *D. hydei* populations. *Proc. VII, Int. Cong. Genetics*, 1939, p. 268.

VAVILOV, N. G., 1922.—The Law of Homologous Series in Variation. *Jour. Genetics*, XII, p. 47.

WADDINGTON, C. H., 1939.—*Introduction to Modern Genetics*, p. 270. London.

WRIGHT, S., 1935.—A mutation in the guinea pig. Genetics, XX, p. 84.