HYBRIDISATION AND CROSS-BREEDING AS A METHOD OF SCIENTIFIC INVESTIGATION

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In this talk, given in 1899, before Mendel's work had been rediscovered, Bateson gives his vision of what kind of research will be necessary to shed light on the processes of inheritance and evolution:

> What we first require is to know what happens when a variety is crossed with its nearest allies. If the result is to have a scientific value, it is almost absolutely necessary that the offspring of such crossing should then be examined statistically. It must be recorded how many of the offspring resembled each parent and how many shewed characters intermediate between those of the parents. If the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect of each of those characters separately.

One would be hard pressed to provide a better anticipation of the experimental approach of Mendel. Small wonder that Bateson, upon encountering Mendel's work, quickly became convinced that the correct method for studying inheritance was finally at hand.

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It is with a special pleasure that I accepted the kind invitation of the Council to address this Conference of persons interested in hybridisation. Of all the methods which are open to us for investigating the facts of Natural History there is perhaps none which is more likely to bring forth results of firstrate importance. Not only is the field a vast one, but the work is ready to hand. Though the patience and labour needed are very great, the practical methods are simple, and can be in many cases carried out by any person who has leisure and is able to carry out anything accurately. Leisure, accuracy, and a garden of moderate extent are almost the only equipment necessary for such work. On the other hand, the scientific importance of the results to be obtained is transcendent.

It is perhaps simpler to follow the beaten track of classification or of comparative anatomy, or to make for the hundredth time collections of the plants and animals belonging to certain orders, or to compete in the production or cultivation of familiar forms of animals or plants. But all these pursuits demand great skill and unflagging attention. Any one of them may well take a man's whole life. If the work which is now being put into these occupations were devoted to the careful carrying out and recording of experiments of the kind we are contemplating, the result, it is not, I think, too much to say, would in some five-and-twenty years make a revolution in our ideas of species, inheritance, variation, and the other phenomena which go to make up the science of Natural History. We should, I believe, see a new Natural History created.

It seemed to me that I could not better make use of this opportunity than by indicating, as far as I can, some of the aims which I think a worker in this field should put before him, and the class of work which, as it seems to me, is most likely to prove fruitful in bringing about the result I have indicated.

The problem, it is assumed, on which all such work is to be brought to bear is the *problem of species.*

I must ask you for a moment to consider the present position of knowledge in regard to Evolution and the nature of Species—for it is with a clear reference to the problem of species that breeding experiments, in the first instance, should, in my opinion, be undertaken. We see all living nature—animals and plants— divided into the groups which we call *species,* groups often so sharply marked off that there can be no doubt where they begin and end; groups often, on the other hand, so irregularly characterised that no two people would divide them alike. What are the causes that brought this about and keep it so? What are the facts underlying this phenomenon of *species?* For phenomenon it is; and, believe as we may that all these forms are related in descent, there they are now, grouped into species as we know. How did this come about?

We all know the accepted view. We start from the fact that, since of all forms of life many more are born than can possibly survive, some—indeed, nearly all—must perish and leave no descendants. Next we observe the fact of Variation—that even the offspring of the same parents are never precisely alike, but vary. Now, since all cannot survive, it is clear that different individuals have a different chance of survival and of being represented by descendants. For each individual this chance will depend on the degree to which its structure and aptitudes fit it to bear its part in the struggle to which it is exposed. Briefly, *on the whole* the fittest will survive and breed.

Lastly, as the places in life that the organisms fit are diverse, so the forms of the surviving organisms are diverse too.

Everyone who cares at all for Natural History knows this reasoning, and knows also the difficulties by which its application to the facts of Nature is beset—how simple the theory seems when thus stated in general terms, but how hard it is to apply it in detail to a particular case.

Of all these difficulties the most serious are two. The first is the difficulty which turns on the magnitude of the variations by which new forms arise. In all the older work on evolution it is assumed, if the assumption is not always expressly stated, that the variations by which species are thus built up are *small.* But if they are small, how can they be sufficiently useful to their possessors to give those individuals an advantage over their fellows? That is known as the difficulty of *small or initial variations.*

The second difficulty is somewhat similar. Granting that variations occur, and granting too that if they could persist and be perpetuated species might be built up of them, how *can* they be perpetuated? When the varying individuals breed with their non-varying fellows, will not these variations be obliterated? This second difficulty is known as that of the *swamping effect of intercrossing.* Now on each of these two points the work of the hybridist and the experimental breeder comes in exactly. It is he who can see the variations arise, and can note their size and find out exactly how large they are—whether they am great or small—whether offspring do really differ but little from their parents, or whether, in certain cases and in respect of certain characters, the differences in variation may not be very great and definite; whether, also, the supposed swamping effect is a real one or not, or to what extent it is real, and in regard to what characters.

I need not tell a body of persons, most of whom have themselves made experiments of this kind, that in numberless cases both great and thoroughly definite variations do occur. This much every practical man now recognises. But we are far from knowing which kinds of variations may thus be definite and palpable, and which are not. All we know is that both large variations and small variations occur, some in one character and others in other characters, and that characters which in one species may vary greatly and suddenly, in other species vary only slowly or hardly at all. All this is a matter which comes daily under the observation of the breeder—especially the cross-breeder of plants or of animals. It is to him that we look for first-hand evidence as to the *magnitude of variations.*

At this point a word of caution is needed. All those present are aware of the great and striking variations which occur in so many orders of plants when hybridisation is effected. As everyone knows, it is to those extraordinary “breaks” that we owe perhaps the majority of our modern flowers. Such, for example, are Narcissus, Begonia, Pelargonium, Gladiolus, Streptocarpus, a great number of Orchids, Rhododendron, the Cineraria, and the like. I mention the Cineraria, because I have personal knowledge of these hybrids, and because I notice that the view that our garden Cinerarias are not hybrids is being again repeated, in spite of the clear evidence, both of history and recent experiment, to the contrary.

With such cases in view some may be disposed to say: “Here are the great and striking variations we are seeking. These new forms are like new species— some would even take rank as new genera. May not the natural species have arisen in like manner by hybridisation?” The answer to this question, however, is almost certainly *No.* And herein I believe most, if not all, professed botanists and zoologists will agree. To go into the matter fully here is impossible; hut for many reasons, most of which have often been repeated, there is, I think, no good evidence for supposing that any natural species, whether of animal or plant, arose by direct hybridisation. Tempting as it may at one time have been to hope that we should thus get a short cut to the origin of species, few, I think, are now sanguine of such an issue. It is not in this direction that we can look for that advancement in knowledge which I believe will surely come from the work of the cross-breeder.

I am far from saying that these striking hybrids are without scientific interest, or that they have no bearing on the problem of species. I wish only to say that it is pretty clear that they have not the direct bearing which they would have if it could be supposed that natural species arose as similar hybrids.

The interest in the cross-breeder's work lies, as I think, in a somewhat different field. Whatever view we adopt of the origin of species—provided that we believe in the doctrine of Descent at all—we believe that every species has been actually produced from something like itself in general, though different in some particular. Wherever these two closely allied varieties exist, the problem of species is presented in a concrete form: How did variety *A* arise from variety *B*. or *B* from *A*, or both from something else? This question involves two further questions:

1. By what steps—by integral changes of what size—did the new form come into being?
2. How did the new form persist? How was it perpetuated when the varying individual or individuals mated with their fellows? Why did it not regress to the form from which it sprang, or to an intermediate form?

To those who admit this reasoning it will be clear that the whole question of the origin of species turns on the relationship of each species or each variety to its *nearest allies*. We may not yet have an authentic case of a nascent species that will satisfy all doubts, but unquestionably we have lots of nascent varieties. If only we make it our business to observe the way in which these nascent varieties come into being, and especially what happens when these varieties are crossed with their nearest allies, we shall have material from which to answer the main questions of which the Species problem consists.

It is only quite lately that any systematic study of such variations has been undertaken from the point of view of the evolutionist, and already some very clear results have been perceived.

As the first difficulty in applying the doctrine of Descent turned on the magnitude of variations, so, as soon as careful study of Variation is begun it is found that large and distinct variations are by no means rare, and that in certain classes of characters they are indeed the rule. To this class of variation, in which the variation is found already at its beginning in some degree of perfection, I apply the term *discontinuous*.

We are taught that Evolution is a very slow process, going forward by infinitesimal steps. To the horticulturist it is rarely anything of the kind. In the lifetime of the older men here present it is not Evolution but Revolution that has come about in very many of the best-known Orders of horticultural plants. Even the younger of us have seen vast changes. It may have seemed a slow process to individual men in the case of their own speciality. It may have taken all their lives to obtain and fix a strain; but in Evolution that is nothing. It is going at a gallop!

Whenever, then, it can be shown that a variation comes discontinuously into being, it is no longer necessary to suppose that for its production long generations of selection and gradual accumulation of differences are needed, and the process of Evolution thus becomes much easier to conceive. According to what may be described as the generally received view, this process consists in the *gradual* transition from one normal form to another normal form. This supposition involves the almost impossible hypothesis that every intermediate form has successively been in its turn the normal. Wherever there is discontinuity the need for such a suggestion is wholly obviated.

The first question was: How large are the integral steps by which varieties arise? The second question is: How, when they have arisen, are such variations perpetuated? It is here especially that we appeal to the work of the cross-breeder. He, and he only, can answer this question: Why do not nascent varieties become obliterated by crossing with the type form?

If you study what has been written on these subjects you will find it almost always assumed that such blending and obliteration of characters is the rule in nature. Whole chapters have been compiled with the object of showing how, in a world in which there is such complete blending, evolution might still go on. There has been a word invented to expressly denote this kind of blending; the word is *Panmixia*, a word barbarously and incorrectly formed to denote an idea which is for the most part incorrect likewise. For if instead of abstract ideas the facts of cross-breeding are appealed to, it is found that so far from this blending and gradual obliteration of character being the rule, it is nothing of the kind. In many characters, on the contrary, it is at once found on crossing that the varying character may be transmitted in as perfect a degree as that in which it was found in the parent. It need scarcely be said that there are many structures and conditions which do not thus retain any integrity when crossed, but there are very many that do. Which characters are thus unblending, and which blend, must be determined by careful cross-breeding; and this knowledge can be discovered in no other way.

The recognition of the existence of discontinuity in variation, and of the possibility of complete or integral inheritance when the variety is crossed with the type, is, I believe, destined to simplify to us the phenomenon of evolution, perhaps beyond anything that we can yet foresee. At this time we need no more *general* ideas about evolution. We need *particular* knowledge of the evolution of particular forms. What we first require is to know what happens when a variety is crossed with its *nearest allies.* If the result is to have a scientific value, it is almost absolutely necessary that the offspring of such crossing should then be examined *statistically*. It must be recorded how many of the offspring resembled each parent and how many shewed characters intermediate between those of the parents. If the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect of each of those characters separately. Even very rough statistics may be of value. If it can only be noticed that the offspring came, say, half like one parent and half like the other, or that the whole shewed a mixture of parental characters, a few brief notes of this kind may be a most useful guide to the student of evolution. Detailed and full statistics can only be made with great labour, while such rough statistics are easily made. All that is really necessary is that *some* approximate numerical statement of the result should be kept. The horticulturist makes a cross: he is perhaps obliged by want of time and space simply to keep what he wants and throw the rest away; but sometimes surely he might put down a few words as to what that “rest” consisted of. If he would do so he would have the gratitude of many a student hereafter. On looking through the literature of hybridisation one is saddened by the thought that while so much skill and money and effort have been expended, for want of a very little more attention to recording, immeasurable opportunities have been missed.

We have seen that it is likely that those experiments will be found the most fruitful which deal with the relationship subsisting between a given variety or species and its nearest allies. The essential problem of evolution is how any one given step in evolution was accomplished. How did the one form separate from the other? By crossing the two forms together and studying the phenomena of inheritance, as manifested by the cross-bred offspring, we may hope to obtain an important light on the origin of the distinctness of the parents, and the causes which operate to maintain that distinctness.

Useful contributions to the physiology of inheritance may no doubt be made by experimental crossing of forms only remotely connected. Such work, however, will not supply the particular kind of evidence most needed. This can only be got by an exhaustive study of the results of cross-breeding between various forms whose common origin is not very distant. Such experiments must, besides, be repeated sufficiently often to give a fairly extensive series of observations on which to base conclusions. Anyone, therefore, who wishes to work on these lines would do well to restrict himself to an examination of the transmitting properties of a small group of closely allied varieties or species, and to explore these properties thoroughly within that group.

Cross-breeding, then, is a method of investigating *particular* cases of evolution one by one, and determining which variations are discontinuous and which are not, which characters are capable of blending to produce a mean form and which are not. It has sometimes been urged as an objection against this method of investigation that the results are often conflicting. It has been said that such work will only lead to accumulations of contradictory evidence. It is, however, in this very fact of the variety of results that the great promise of the method lies. When varieties and species are tested by this method it is found that their mutual relations are by no means alike, and properties are disclosed which can in no other way be revealed.

In illustration, I will refer to three cases of hairy and smooth varieties. In each case there is a well-marked discontinuity between the two varieties; but, as is strewn by the evidence obtained by cross-breeding, the nature of the relationship[1] of the two forms to each other is different in each case, and the distinctness is maintained! by different means.

The plants (produced at the meeting) illustrating the following observations were raised by Miss E. R. Saunders, of Newnham College, Cambridge, who is carrying out a large series of experiments on this subject.

The first case is that of *Matthiola incana,* a hoary species, and its smooth variety known in gardens as the wallflower-leaved Stock. Experiments in crossing these two forms were made by Brevor Clarke, and briefly described by him in “Report of botanical Congress”, 1866. Amongst other things his investigations shewed that on crossing these two varieties the offspring consisted entirely of completely hoary and completely glabrous individuals, no intermediate being present. Miss Saunders' work entirely confirms this result. The type-form used by her was procured from seed of presumably wild specimens growing in the Isle of Wight. The glabrous variety was the ordinary garden form the origin of which is not known to us. In this case discontinuity is manifested in its simplest form.

The second example is that of *Lychnis diurna.* There, again, the normal is hairy. A glabrous variety was found by Professor de Vries, and was by him crossed with the type. All the first generation of cross-brads inherited the hairiness in its complete form. When, however, these plants were crossed again with the smooth form, the result was a mixed progeny, of which some were hairy and others smooth: The same result also occurred when the cross-bred plants were bred with each other. Professor de Vries kindly sent seed of his glabrous form to Cambridge, where Miss Saunders repeated the experiments with the same results. In all the cases of mixed progeny there is a sharp discontinuity.

The third case is that of *Biscutella laevigata.* A full account of this important case was published by Miss Saunders in *Proc. Roy. Soc*. LXII, 1897, II. Briefly the facts are as follows. The species is common as a hairy plant throughout a great part of the Alps. In a few localities a variety occurs having the *surfaces* of the leaves quite

[1] The term “relationship” is somewhat misleading, but I cannot find a better. It is used to denote not simply the blood-relationship of the forms to each other, but those physiological relations subsisting between them which are manifested by experimental crossing. The word is thus used in a sense similar to that which it bears when we speak of the chemical relations of one substance to another.

devoid of hairs. (There are almost always some hairs on the margins and leaf-teeth.) When present, this smooth form occurs abundantly, mixed with the hairy type. Intermediates are of rare occurrence. If plants of the two kinds breed freely together, as in the natural state we must suppose they do, how is the sharp distinction in their respective characters maintained? The result of artificial cross-breeding went to shew that of the young seedlings of mixed parentage some were hairy, some smooth, and a good many intermediate. But as these seedlings grew, the hairy and the smooth retained their original characters, while the intermediate ones gradually became smooth. The transition was not effected by actual loss of hairs, but after the first few leaves of intermediate character the leaves subsequently produced were smooth.

In all these three cases there is discontinuity, the intermediates between the varieties being absent or relatively scarce. Nevertheless, on examination it is found that the discontinuity is not maintained in the same way in the different cases. The transmitting powers of the one variety in respect of the other are quite different in each case, and it must, I think, be admitted that we have here a fact of great physiological significance. In each of the three cases enumerated the two varieties are seen to stand towards each other in a different relation, and in each the mechanism of inheritance works differently.

From facts like these we perceive how imperfect is the survey of the characteristics of species and varieties which can be obtained by the ordinary methods of anatomy and physiology. There can be no doubt that, tested by the method of breeding and by study of the transmitting powers, the relation of varieties and species would be shewn in an entirely new light. We are accustomed to speak of "variability" as though it were a single phenomenon common to all living things; and just as the older naturalists spoke of *species* in general as all fixed and comparable entities, so many of the present evolutionists speak of "varieties" in general as all comparable. This is a mere slurring of the facts. Not only must variability in respect of *different* characters be a manifestation of distinct physical processes, but, as we have seen, variability, even in what appears to us to be the same character, may be a wholly different matter.

Our business, then, is to test and examine these different kinds of variabilities according to their behaviour when the different varieties are crossed together. By this means we are enabled to investigate the properties of organisms in a way that no other method provides.

If I may be allowed to use a metaphor taken from chemical science, regarding species and varieties as substances, we may investigate their properties and their powers of entering into genetic combinations, just as the chemist investigates the powers of his bodies to enter into chemical combinations.

To lump all the different manifestations of variation together as "varieties", and to rest there, is to give up in despair.

Similarly, it is certain that what we call "species" is a mixture of different phenomena, or rather of different classes of phenomena confounded under one name. I look to the study of cross-breeding to unravel that extraordinary mass of confusion. I look to this method of investigation to deliver us from the eternal debates on the subject of what is specific rank and what is not.

On the one hand we have at the present day many who devote themselves entirely to discussions of this nature, though they know in their hearts that their views correspond to no natural fact whatever. On the other hand, many in disgust and impatience reject the whole thing. "There is no such thing as species", say they. Both sides are surely wrong: there is such a thing as species, and we have to find out what are the properties of species.

It is true that, as to most species and varieties, artificial breeding is impossible, but in numerous cases a beginning can be made. Take merely the phenomenon of local varieties, or local species, or local races, about which such weary discussions have arisen. Each of these offers a particular example of the Evolution problem. In numbers of such cases an investigation of the behaviour on crossing could be practiced, and a very few such experiments would, I venture to predict, do more to establish true views of the relation of species and varieties than the labours of systematists will do in ages.

To come much nearer home, we do not know for certain the true relationships—in this special sense—between the varieties of the commonest domestic animals and plants. For example, I have been trying to investigate these relationships between the several kinds of comb in domestic poultry. I have thus far found no one who can tell me for certain what happens when they are crossed. The various forms of comb in our breeds of poultry—simple comb, pea-comb, rose-comb, etc.—are important structural features, which differ from each other very much as many natural species do. The answer generally given is that the result of such crossing is uncertain—that sometimes one result occurs, and sometimes another. This, of course, merely means that the problem must be studied on a scale sufficiently large to give a statistical result. There is here an almost untouched ground on which the properties of specific characters can be investigated. Many similar examples might be given.

True and precise experiments in these fields so ready to our hand have never been made. We appeal to those who have the opportunity to use it for the advancement of this fascinating line of research. It is delightful to form great collections of animals or plants, and to “bring out a novelty” may be an exhilarating sensation; but if anyone will abandon these well-worn pursuits, and devote himself to experimental cross-breeding, he will soon have his reward, for no line of research is likely to prove more fruitful.