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A TAXONOMIST'S EXPERIENCE WITH HYBRIDS IN THE WILD[1]

By Dr. KARL M. WIEGAND

CORNELL UNIVERSITY

IT is with much trepidation that I approach this subject in an audience that is doubtless more deeply informed on the recent phases of genetics than I. The only justification for such audacity is that possibly some of the observations from another angle may supplement the splendid work of modern students in that now highly specialized field. I shall not attempt, however, a very deep genetical discussion of the observations made.

In his every-day experience with plants in the field the taxonomist is accustomed to think of the species in certain groups as clear cut and easy to work with, while other groups are difficult and the species more or less confused with no sharp boundaries. Much thought has been given at different times to the question as to why there is this difference between groups and what is its true phylogenetic significance. Long ago, among the special creationists there seemed to be no explanation other than that at the moment of creation the plans for these difficult groups had not been sufficiently worked out and perfected. Following the general acceptance of the theory of evolution, it seemed that in certain groups, species were perhaps in the making, through active variation, with the lines not clearly drawn as yet by natural selection. The more confused groups were therefore the newer groups. There still seems much reason for thinking this to be true in a general way.

That hybridity played any important part in causing the difficulty of species delineation in these groups was given little attention and rarely if ever suggested. The occurrence of hybrids in the wild was, in those days, thought to be a rather rare occurrence. In

[1] Address of the retiring vice-president and chairman of the Section for the Botanical Sciences, American Association for the Advancement of Science, Pittsburgh, December, 1934.

Gray's Manual (Edition 5), we find hybrids scarcely mentioned except in one genus, Quercus, where 5 were listed. In the 6th edition this had been increased to 9, and 9 hybrids in Carex were discussed. In this edition also mention was made of numerous hybrids in Salix. At that time there seems to have existed a rather indefinite prejudice against the hybrid. The hybrid tended to disorganize and do violence to the orderly classification of nature. So few were recognized, too, that the burden of proof was always with him who assumed the hybrid explanation. The matter was still more complicated by the lack of criteria for recognizing hybridity and to some extent also by the taxonomist's unfamiliarity in many cases with the behavior and characteristics of hybrids in cultivation. Some taxonomists apparently held the view-point that legitimate species should be difficult to cross, and therefore that wild hybrids should not be expected.

With the discovery of Mendel's studies on peas, the whole outlook toward hybridity began to change. These studies stimulated enormously an awakening interest in the problems of inheritance, and the whole modern science of genetics is the outcome. Along with this too was an awakened interest in the improvement of cultivated plants by breeding methods. One general result has been a more or less changed regard for the hybrid itself and it is no longer the outcast that it formerly was, but is full of interest as exhibiting some of the interesting and vital discoveries in heredity. In fact one author, Lotsy, has gone so far as to suggest the all-importance of the hybrid as the only source of new species in nature.

At about the time that Mendel's work was discovered by DeVries and others I became interested in the taxonomy of the genus Amelanchier, which presented forms in the region where I was then living that were at variance with the treatment of the genus in the different manuals. A wealth of forms was found there in central New York, but no satisfactory disposition of them could be made. Some years later, on removing to the vicinity of Boston, the same experience was repeated. Two summers spent in Newfoundland at about this time furnished a similar experience. In this latter country Amelanchier was abundant, but it seemed almost as though no two individuals were the same. A certain botanist who had given some attention to the genus stated to me that he seriously doubted whether species in the accepted sense existed in this genus at all. This general uncertainty induced me to seriously undertake a study of the genus to see if it were possible to discover the actual situation. Besides notes made in the field, more than a thousand herbarium specimens of East American Amelanchiers were assembled from different herbaria, and much time for a year was spent on the problem. Many sortings of this material were made, based on different structural characteristics, but at first without clarifying the situation.

The increasing interest in hybridity due to Mendel's work caused me at length to wonder whether crossing could have anything to do with the Amelanchier situation. So finally an attempt was made to sort the specimens as though there were a number of true species among them which when crossed with each other in pairs would account for the remaining forms. It was assumed that the true species when found would have certain characteristics, namely, they would probably each offer one or more characters peculiar to that species individually. Each species would also be expected to show a more or less normal range corresponding to the geographical regions of the country, as shown by the ranges of species in other groups. Also each would probably show certain soil and other habitat requirements, a certain period of flowering, and in other ways behave like species in other genera.

It was assumed also that hybrids would show certain peculiarities. They would not ordinarily present any new characters, but would simply recombine characters found in the two parent species, or in some cases show a blend of characters. The range too would tend to be small, as the hybrids presumably would not have had time to spread over wide areas, and thus their ranges might not follow the geographical areas, as possibly they had not spread that far. Also, hybrids would not be found outside the range of the two supposed parents.

Several sortings were made on this basis, but still with unsatisfactory results as far as the above points were concerned. Then suddenly a sorting was made that gave six piles of specimens. Each of these piles was essentially uniform and showed all the characteristics of a true taxonomic species as judged by the criteria just mentioned. In addition, there remained a seventh pile with quite different characteristics; it was not homogeneous as to character, it did not show new characters not present in the other six piles, and as far as distribution was concerned it was a mass of heterogeneous material. All the specimens in this pile, however, could be interpreted as crosses between some two of the other six piles.

We had then a rational disposition of the material, the first so far obtained. Here there were six good species similar to those in other groups, and the remaining material could be interpreted as hybrids of these species. The hybrid group, to be sure, was larger than might seem reasonable in nature, since it comprised about one third of the whole number of specimens. This, however, could be explained by the fact that while some of the six piles had been recognized before as common species and were familiar to many collectors, all the hybrids were peculiar unidentifiable specimens and therefore were collected much more frequently than their comparative abundance in nature would lead one to expect.

Here we have an interpretation of hybridity based on what is really circumstantial evidence. Of course, the surest way to determine whether a plant is a hybrid is by breeding it to determine whether the characters behave in succeeding generations as hybrid characters should. I hear some of you ask why this has not been done. Most groups studied for revision by the taxonomist cover wide areas of country which, because of time and cost, he can visit only rarely and perhaps then not at the exact season for critical study of his group. He is forced, therefore, to depend to an undue extent on herbarium specimens. These obviously can not be bred, and indeed frequently the locality from which a particularly interesting plant came can not be visited. The only recourse is to depend upon circumstantial evidence of the sort just outlined. However, this does not mean, it seems to me, that such evidence and the conclusions drawn are necessarily of no value. In the few cases where breeding has been done, the original interpretations of the taxonomist have been generally supported. But if the plants can not be bred, it is still often very helpful to visit the locality from which a supposed hybrid was obtained. We may find not only the necessary parents but also other hybrid individuals showing other combinations of the parental characters. Some of these may be brought home and themselves bred. Also artificial hybrids between the supposed parents made in the garden will furnish material for comparison. Breeding, however, requires a certain special technique and space for growing the plants—requirements which render breeding by the taxonomist often very difficult. After all, in the study of large groups, chief dependence will still have to be placed on information gained from herbarium specimens. It has been suggested, to be sure, that hybrids may be told by the proportion of sterile pollen, and since that could probably be determined, at least roughly, in herbarium specimens, it might be an additional source of evidence. It is my belief, however, that investigations have tended to show this criterion to be of little use. Many apparently normal species often show as high as 50 per cent. sterile pollen (Erlanson on Rosa) while some hybrids have good pollen. Ecological conditions, also, appear to affect the viability of the pollen.[2]

Since the work on Amelanchier, the same problem has been met in the study of two groups of white asters. The same conditions were encountered, the same methods used, and the same conclusions reached as in the former case. In each of the groups of asters three or four species were found, together with a mass of specimens which could be reasonably accounted for only on the assumption that they were of hybrid origin with these species as parents. As in Amelanchier, the number of such hybrid specimens in the herbarium was greatly in excess of what one would expect from observations in the field, and the explanation is probably the same as in that case.

While these three studies have seemed to lead directly to the belief that hybridization in nature is a common phenomenon, other studies on other groups would seem to lead to the opposite conclusion. A revisionary study in two groups of Carex has shown no signs of hybridity. Neither were signs of hybridity found in the *Eupatorium purpureum* group, nor in Galium. Hybridization in the wild is therefore much more frequent in some groups than in others. It would seem that the Rosaceae in particular are liable to hybridize, and other taxonomically difficult genera in this family, such as Rubus, Rosa, Crataegus and others will probably be found to offer many cases of natural hybrids.

The query now arises: Are hybrids constantly produced in these groups, and, if not, what are the controlling factors? My experience tends definitely toward the conclusion that between certain species a great burst of crossing may occur locally all at once, and that this may or may not continue thereafter for a period of time. Lotsy in his field studies in South Africa has reached essentially the same conclusion. Over a limited area one will often find abundant hybrid individuals showing all manner of combinations of the characters of two parent species. The lay botanists get the impression that here the genus is "running wild." Elsewhere over large areas, even miles in extent, there may be no evidence of crossing whatever.

But what causes plants to hybridize thus locally and suddenly? My own observation seems to indicate that disturbance of the environment has something to do with the matter, and on this the following cases may throw some light. In Newfoundland a railway crosses the island. Near the railway the forest has been largely destroyed by fire or through logging operations. Tracts miles in extent are covered with dead brush and dense scattered thickets of scrub growth. Amelanchier is common in this region, but taxonomically it was found to be a mess, as almost every individual seemed different from its neighbor. In less disturbed areas the plants were more uniform. In the detailed study of this genus already alluded to, it appeared that many of the plants in the disturbed areas were hybrids, and the more uniform strains in

[2] See C. L. Huskins, SCIENCE, 69: 399, 1929.

the less disturbed regions were true species found generally in eastern North America.

Again, on the Blue Hills south of Boston, the forest has largely disappeared. Frequent fires have ravaged the region, and when visited several years ago presented alternating areas of bare rock, brush and open thicket. Amelanchiers were common, but few individuals were like any known species or like each other. Here also a peculiar micropetalous form occurred, previously noted by Dr. Robinson. Studies seemed to show that these aberrant forms were hybrids of three species occurring in the neighborhood, of which two were dry ground species and one an inhabitant of the swamps at the base of the hills. The micropetaly was due apparently to the effect of the fire, probably on the roots.

In eastern Maine near Pembroke Rubus was very abundant. In one locality the railway ran for a long distance through a lowland piece of woods. The forest came up to the right of way, which latter was kept cleared and mowed each season. Close to the track the ground was weeded frequently and therefore was very much disturbed. Along the border of the weeded zone prostrate, semi-prostrate and arching individuals of Rubus occurred in considerable numbers. These were "queer," many of them being unlike anything known to us. In the mowed zone there were fewer individuals and they were less queer, while over near the fence and bordering the woods the plants were, for the most part, clearly straight species with which we were familiar. Most, if not all, of these queer forms could be interpreted as crosses between the species near the woods, as they seemed to show only combinations of characters existing in these species. Not being a specialist in Rubus, I would hesitate to say that the aberrant forms were all hybrids, but they were very suggestive.

Another genus that has caused no end of trouble to the taxonomist is Crataegus. Here, in many parts of the eastern states, individuals of this genus occur often in very great numbers, forming extensive stands. The wealth of form is frequently very great, giving the impression at times that no two plants are alike. These individuals have been treated very differently by different taxonomists. Dr. Sargent, in his account of Crataegus in New York State, listed about 218 species, while Eggleston for the same area recognized only 38 species. Sargent, it is said, refused to believe that hybrids occur in Crataegus, or occur but rarely, while Eggleston is inclined to admit that hybrids are frequent or at times common. The species of Crataegus are chiefly pasture weeds in New York State, frequently destroyed by the farmer and subject to grazing by cattle. They can be said, therefore, to live under disturbed conditions. I suspect that the early botanist, before the country was settled, would have found no such wealth of form as exists to-day.

Hybrids in the field then tend to occur locally at some particular time and often in considerable abundance. While the cause of this is still obscure, a very suggestive hypothesis would connect it directly with the disturbed conditions just mentioned. It might well be that these conditions induce irregularities in the time of flowering. If some flowers are produced earlier or later than the normal period for that species, then these flowers might find no pollen from their own species but only that from some other species whose flowering period was earlier or later, as the case might be. Whether this is so has not been determined as yet. In this connection it is interesting that one author at least has cited dichogamy, especially in dioecious species, as a stimulus to hybridization. Obviously these suggestions here offered with regard to the time of flowering should not be given much weight until more evidence is at hand.

As to the significance in evolution and in the species question of this hybridization in the wild, much may be said, and much has been said. The literature of genetics contains many recent contributions to this subject, but unfortunately there are as yet very discordant views. At present there seem to be two generally accepted sources of divergence between parent and offspring, namely, gene mutation and hybridity. With the first we are not here concerned. In regard to the second, there have been very different viewpoints ranging from the extreme view of Lotsy, who saw no other cause for variation, to that of those who have wholly doubted the importance of hybridity in the production of new forms in nature. The old idea that hybrids are necessarily infertile is of course no longer held, as experiment has shown many cases of fertile hybrids. Reasons for fertility and infertility have been determined in many cases, and in plants the connection with polyploidy has recently been stressed. It is now known also that many hybrids may breed true, either as homozygous segregates or through connection with polyploidy. It is known too that in some genera, as for instance in the *Rosa canina* group, breeding true may occur through an apogamous development of embryos in seeds borne by the hybrid. But breeding true as recessives has been over-emphasized, it seems to me, as a cause of fixed races, as not all recessive characters are homozygous at the same time, and while one character has become pure many of the other innumerable characters going to make up the species concept are still heterozygous. Of course eventually one may get individuals having the composition a b c d e f g h i j, etc., but the chance is small. To be sure, if the plants were always selfed the time required might not be so long, but few species are always selfed.

While fixed races can thus probably be produced by crossing, the question as to whether new species are formed in this way is another problem, and the evidence is not at all clear as yet. Are new characters thus created? Mendel in his experiments with peas obtained only recombinations of parental characters in the offsprings, and not new characters. In many cases it is now known that blends occur. To what extent they occur in nature is not yet clear. Casual observation does not easily discriminate between blends and the recombination of numerous closely related characters. Brainerd and Gershoy apparently found only blends in the F_1 generation of their violet hybrids, and often blends also in succeeding generations. While in a sense blends are new characters, they do not step outside the morphological range of the two parents, and they are doubtfully permanent. Where they occur they tend more toward a smoothing out of variation than toward wholly new forms. While geneticists have discovered some cases where new characters have appeared in hybrids, as for instance in Bateson's sweet peas, in Emerson's corn plant colors and in the walnut comb of fowls, I am not yet convinced that it is a sufficiently common occurrence to account, even in geologic time, for the great morphological diversity in plants. Many of the cases observed have had to do with color and not with structure, and are clearly due to the interaction of genes present in the parents rather than to new hereditary factors originating in the hybrids themselves.

Another serious difficulty in the way, if we are to consider hybridity as an important cause in the origin of species, is the dearth of evidence that it so operates in nature. I have already called attention to the situation in Amelanchier. After the hybrids were recognized and segregated there remained six or seven good species with normal ranges coinciding in general with the geographical areas in eastern North America, and fitting in with the ranges of other plants. The hybrids were usually local. Circumstantial evidence, therefore, seemed to indicate that these true species had been in existence a long time, during which they had spread over wide areas, as for instance from Newfoundland to Georgia and Minnesota—over all the area having suitable habitat conditions. They were old enough to have become more or less static as far as distribution was concerned. The hybrids seem like swarms of bees, buzzing around for a time, only to disappear, leaving the fundamental species to continue through the ages.

Professor Fernald has called attention to the fact that apparently in glaciated Nova Scotia only one weak species has been produced in the 25,000 or 30,000 years since the Wisconsin glaciation, and that in the glaciated coastal region of eastern North America *Bidens hyperborea*, occurring in several isolated localities, has maintained its specific identity during this same period. Though it belongs to a notoriously plastic genus, it has shown at the most only varietal deviations in these isolated habitats. In fact a geographer is led almost inevitably to feel that nearly all our east American plant species go back to the glacial period and probably far beyond. It can not be denied that species may have arisen through hybridity, quite possibly in the ways suggested by many geneticists, but one can not become very enthusiastic. At least, it seems evident that species are not being formed every day, or even every year, or even every century, as some enthusiasts are inclined to think.

What, then, becomes of the hybrids that from the standpoint of geological time are being produced in hordes? This to me is one of the interesting problems in evolution, second only to the problem of the origin of species in the first place. Geneticists have made suggestions in this connection. There would be, for instance, much sterility which would limit the number of offsprings. The hybrids would be free to cross again with the parent species in nature and homozygous recessives would be swamped. These recessives too would be weak in the struggle for existence. In these recessives, while they would be homozygous and recessive to one character, they would often be not so to others unless after a very long period of time and then only in comparatively few individuals. Most hybrids would tend to disappear therefore. The occasional production of stable polyploids would reduce this general tendency, but probably not to a marked degree. These genetical explanations of disappearance seem not quite sufficient to wholly account for the phenomenon, and we must await further studies.

One other problem remains in connection with wild hybrids. How shall we treat them taxonomically? Many systematic botanists have been loath to recognize them at all, or to admit that crossing occurs in nature. In recent years the belief in natural hybridization has greatly increased. A rational outlook, however, has been prejudiced by the unscientific attitude of some of these enthusiastic taxonomists. Many highly improbable and rash interpretations have been made that did not accord with the known facts. Since breeding is usually impossible and our decisions must be based largely on circumstantial evidence, special care should be used to see that our deductions are reasonable. The least that can be asked is that these deductions should be based only on careful and painstaking analysis of the evidence. Some recent writers have even assumed crossing between parents that do not grow in the locality or even in that part of the country. Often general impressions and not an analysis of characters have been sufficient to impress these enthusiasts. The only result is to discredit taxonomy.

But equally unfortunate is the attitude that would prohibit the recognition of natural hybridization except in hybrids actually bred genetically. The argument that a supposed hybrid, unbred, is merely a matter of personal opinion, and therefore should not be recognized, is invalid, for so are species, genera and families matters of personal opinion. In any taxonomic manual the groups there presented represent the author's interpretation of nature and nothing more. These groups are based likewise on circumstantial evidence, since he has not seen these species arise in nature, and represent only the conclusions reached from careful study of existing material. Why, then, should the taxonomist be adverse to the recognition of hybrids, who is perfectly willing to accept innumerable new species on much less reasonable ground? Taxonomists who do not recognize hybrids are often forced to treat such suspected forms as species. They are willing to assume them to be species until some one proves them to be something else, thus placing the burden of proof on the other fellow. I, personally, belong to that benighted group of taxonomists, who believe that new species should not be proposed as such until the author can not reach any other conclusion. Is it not our duty to science, to workers in other fields and to our fellow taxonomists not to clutter up our subject with endless names and half-baked concepts which seem only to confuse and to cause resentment and to pass the buck? The science of taxonomy stands too low now in the estimation of general workers.

How, then, should hybrids be named? The recognition of supposed hybrids as hybrids should not necessarily increase the number of names which we all deplore. It is my preference to designate ordinarily such a plant by the expression *Quercus bicolor* × *macrocarpa* and not by a new name. The only exceptions would be a few hybrids that in horticulture have acquired well-known specific names. Into this condensed designation "*Quercus bicolor* × *macrocarpa*" we would always read the expression, "A probable hybrid of *Quercus bicolor* and *Q. macrocarpa*, according to my interpretation" unless the hybrid had been actually demonstrated by breeding or synthesis. But so do we also read into the designation "*Q. macrocarpa* Michx." as a species, the statement, "A species, *Q. macrocarpa* in the sense of Michaux as interpreted by me." I can not help but see at least a practical difference between the causal more or less evanescent and temporary hybrid and the fundamental established species reaching back perhaps to the glacial epoch or beyond. The six fundamental species in the Amelanchier study did not seem in the same category with the hybrids, which, when eliminated, revealed them. I prefer to restrict the binomial to these older fundamental units for clearness and also on sentimental grounds.

In conclusion it may be asked again what relation then this experience with hybrids in the wild bears to the problem of the origin of species. As already mentioned, Lotsy was of the belief that hybridity is very likely the sole cause of the origin of new forms. Most biologists, I believe, are not ready to take a stand so extreme, but many students of genetics feel that the stable hybrids produced in their experiments represent at least one way by which new species may arise. While I would not really question this last statement, the point interesting to me is the almost[3] total lack of support for this view in our experience with the wild hybrids. As pointed out, the mass of hybrids in the cases under observation seem wholly casual and in no way to affect the fundamental species, which presumably have existed almost unchanged since the glacial period or before. It is still possible that these fundamental species came about by hybridity, and that others will also, if sufficient geological time is allowed. It would seem, however, that the factors noted by the geneticist ought to produce stable forms much sooner than that, even at the longest. Still another question, of course, is whether hybridity, which combines the genes of two parents, could produce new characters often enough and of sufficient magnitude to account for the great morphological diversity in plants. It is clear, I think, that we have not yet solved the problem of the origin of species.

The observations and view-points expressed in this paper are of course those of one person only, and are presented for what they may be worth. However, the angle from which they are presented is not quite the conventional one, and this may be an excuse for afflicting you with them.

OBITUARY

ROLAND BURRAGE DIXON

ROLAND BURRAGE DIXON, the senior member of the division of anthropology of Harvard University, died on December 19, 1934. He was the greatest ethnographer whom this country has produced. Dixon was born at Worcester, Massachusetts, on November 6, 1875. He took his A.B. degree at Harvard in 1897 and his Ph.D. in anthropology in 1900. From the year of his first degree until his death he was continuously

[3] A few cases: Huskins (*Genetics*, 12: 531, 1931) claims a hybrid origin for *Spartina Townsendii* and Müntzing (*Hereditas*, 14: 153, 1930) describes a hybrid in his cultures indistinguishable from *Galeopsis Tetrahit* L. both morphologically and in chromosome number—a synthetic *G. Tetrahit*. Should be further studied.