

CHAPTER VI.

THE EVIDENCE FROM HYBRIDS.

Importance of the subject—It furnishes a means of analyzing or isolating the influence of each sexual element—Hybrids very variable—Hybrids from domesticated races more variable than those from wild races—The descendants of hybrids more variable than the hybrids themselves—The offspring of a male hybrid and the female of a pure species are much more variable than those of a female hybrid and the male of a pure species—These facts inexplicable on any view, except the one here presented—Reciprocal crosses—They differ in fertility and in structure—The difference is exactly what our theory requires—Difficulty in explaining transmission of characters without fusion—Reversion caused by crossing—Two kinds of reversion—Summary.

THE study of hybrids and crosses is of especial interest to us, since it affords us a means, somewhat imperfect it is true, for recognizing, in the offspring, the structure which it owes to each parent.

In ordinary sexual reproduction between animals or plants of the same race, the parents are almost exactly alike, except for their sexual differences; and as nearly every structural feature of the young is a feature of resemblance to each parent, there can be nothing to show that it is inherited from the one rather than from the other.

When distinct races or species are crossed, the case is somewhat different. It is true that the two parents are still very much alike, for species cannot be made to breed together at all unless they are very closely related. Still they are more different from each other than individuals

of the same species, and the study of crosses and hybrids is therefore a means of separating, to some extent, the influence of one parent from the influence of the other. This is true, however, only with reference to characteristics which are of recent acquisition, for the greater part of the history of two allied species has been the same, and they show in common everything except what has been acquired by each one since they diverged from their common ancestor.

Crossing gives no way of showing whether these common characteristics are or are not transmitted by one parent or the other or by both, but it does give us this information regarding characteristics which appear in one species but not in the other, and it is therefore the best means at our disposal for studying the influence of each parent upon the offspring.

Crossing as a Cause of Variation.

According to our theory of heredity, we can easily see how the crossing of two species or varieties should lead to variability, for when two species or varieties are crossed certain cells of the body will be hybrids between the gemmules of the male parent and the ovarian particles inherited through the female from the egg of the preceding generation. Now the ovarian particle transmits the properties of a cell like that of the female parent, while the gemmule transmits those of a corresponding cell in the father. It is plain that corresponding cells of a female of one species or variety and of a male of another species or variety must be more different from each other than corresponding cells in a male and female of the same species or variety. The hybrid cell formed by their union would, therefore, be expected to differ more from each of them, that is, to vary more than it

does in the offspring of parents of the same variety. It is well known that this is the case; that, in domesticated animals and plants at least, crossing is a great cause—according to some older writers the only cause—of variation.

Darwin says that it is probable that the crossing of two forms when one or both have long been domesticated or cultivated, adds to the variability of the offspring, independently of the commingling of the characters derived from the two parent forms. He believes that new characters arise in this way in hybrids between domesticated forms, forms which have been rendered variable through cultivation, but he doubts whether we have, at present, sufficient evidence to prove that the crossing of species which have never been cultivated leads to the appearance of new characters.

The following illustrations of this law are quoted from his *Variation* (Vol. ii. p. 319):

“Gärtner declares, and his experience is of the highest value on such a point, that when he crossed native plants which had not been cultivated, he never once saw in the offspring any new character; but that from the odd manner in which the characters derived from the parents were combined, they sometimes appeared as if new. When, on the other hand, he crossed cultivated plants, he admits that new characters occasionally appeared. . . . According to Kölreuter, hybrids in the genus *Mirabilis* vary almost infinitely, and he describes new and singular characters in the form of the seeds, in the colors of the anthers, in the cotyledons being of immense size, in new and highly peculiar odors, in the flowers expanding early in the season, and in their closing at night. With respect to one lot of these hybrids he remarks that they presented characters exactly the reverse

of what might have been expected from their parentage.

“Professor Lecoq speaks strongly to the same effect in regard to this same genus, and asserts that many of the hybrids from *Mirabilis jalapa* and *multiflora* might easily be mistaken for distinct species, and adds that they differed in a greater degree than the other species of the genus from *M. jalapa*. Herbert has also described the offspring from a hybrid *Rhododendron* as being as unlike all others in foliage as if they had been a separate species. The common experience of floriculturists proves that the crossing and recrossing of distinct but allied plants, such as the species of *Petunia*, *Calceolaria*, *Fuchsia*, *Verbena*, etc., induces excessive variability: hence the appearance of quite new characters is probable. M. Carriere has lately discussed this subject; he states that *Erythrina cristagalli* had been multiplied by seed for many years, but has not yielded any varieties; it was then crossed with the allied *E. herbacea*, and the resistance was now overcome, and varieties were produced with flowers of extremely different size, form, and color.”

Darwin, therefore, concludes that crossing, like any other change in the conditions of life, seems to be an element, probably a potent one, in causing variability.

The variability of hybrids is quite as explicable by Darwin's Pangenesis hypothesis as it is by our theory of heredity, although I do not see why, on the hypothesis of pangenesis, the hybrid offspring of domesticated forms should be any more variable than those produced between wild species.

The Offspring of Hybrids more variable than the First Generation

There is another aspect of the variability of hybrids which is very remarkable, and which is in perfect agreement with our theory of heredity, but, so far as I am aware, absolutely inexplicable without it.

This is the law that although the offspring of the first generation are generally uniform when two species or races are crossed, the subsequent generations of children produced by these hybrids display an almost infinite diversity of character. (Darwin, *Variation*, ii. p. 321.)

Darwin also refers to this curious law in the *Origin of Species*, p. 260, and attempts an explanation of it. He says: "The slight variability of hybrids in the first generation, in contrast with that in the succeeding generations, is a curious fact, and deserves attention. For it bears on the view which I have taken of one of the causes of ordinary variability, namely, that the reproductive system from being eminently sensitive to changed conditions of life, fails under these circumstances to perform its proper function of producing offspring closely similar in all respects to the parent form. Now, hybrids in the first generation are descended from species (excluding those long cultivated) which have not had their reproductive systems in any way affected, and they are not variable; but hybrids themselves have their reproductive systems seriously affected, and their descendants are highly variable."

According to this view, the variability of the descendants of hybrids is a sort of monstrosity, due to the failure of the reproductive organs to perform their proper functions; ordinary variability is not monstrosity, but is perfectly normal, and as the variability of hybrids

has precisely the same character, I think we cannot regard it as due to unnatural disturbance.

According to our theory, variation is due to the action of changed or unnatural conditions upon certain cells of a preceding generation. Now, as characteristics of both parents are mingled in a hybrid, it must nearly always happen that certain cells with peculiarities of one parent will be in contact with, or will depend in some way upon, cells with peculiarities inherited from the other species. There will therefore be a lack of the perfect adjustment between each cell and its neighbors, which has been brought about in each parent by natural selection, and this imperfect adjustment will cause the cell which is unfavorably placed to throw off gemmules. The cells of the body of a hybrid will therefore be unusually prolific of gemmules, and will transmit variability to later generations.

According to our hypothesis, a hybrid is more likely to transmit variability than a pure species, because more of its cells are placed under circumstances favorable to the production of gemmules.

For the same reason a hybrid between two domesticated or cultivated forms must have more tendency to vary than one produced by crossing two wild species, for the domestic or cultivated parents live under unnatural conditions, and therefore have more tendency than wild species to transmit gemmules, and thus cause variability.

The Sex of the Parent affects the Variability of Hybrids.

I have shown that the body of a hybrid is peculiarly favorable for the production of gemmules, and that, for this reason, the descendants of hybrids are variable

to an unusual degree. Now, if our theory of heredity is true, if the seminal fluid is especially adapted for the transmission of gemmules, while their transmission by an ovum is a matter of accident, the tendency to vary must be transmitted by the male hybrid.

When children are born from two hybrid parents it is impossible to show that the variability which follows comes from the father rather than from the mother, but the subject can be put to a test by crossing the male hybrid with a female of one of the pure species, and the male of one of the pure species with the female hybrid. Neither pure species has any especial tendency to transmit variation, while the male hybrid has such a tendency. If, then, we cross the female hybrid with the male of one of the pure forms, the offspring would not be expected to be unusually variable; but if the male hybrid is crossed with one of the pure females we should expect the offspring to be unusually variable.

Now it is very interesting to find that this actually is the case. Thus Gärtner states (*Bastarderzeugung*, p. 452, 507) that when the seeds of *Dianthus barbatus* were fertilized by the pollen of the hybrid *Dianthus chinensis-barbatus*, the seedlings were more variable than those which were raised from the seeds of the hybrid fertilized with the pollen of *Dianthus barbatus*. Darwin states that Max Wichura obtained the same result with willows. Gärtner concludes from a number of experiments that when a hybrid is used as the father, and either one of the pure parent species or a third species as the mother, the offspring are more variable than when the same hybrid is used as the mother, and either pure parent or the third species as the father.

Darwin's pangenesis hypothesis furnishes no explanation whatever of this curious fact. On the contrary, as

it requires that each sexual element should contain gemmules from every part of the body of the parent, it is directly opposed to any such result, and there is no place for it in any other hypothesis of heredity. Our theory fits it exactly, however, and a more crucial test could hardly be proposed than an experiment like those detailed by Gärtner.

Reciprocal Hybrids.

According to Darwin the two sexes play similar parts in heredity, and any characteristic whatever may be transmitted by either sexual element.

This conclusion is based upon the phenomena of crossing, but a little thought will show that it is impossible, from the nature of the case, to prove it from evidence of this kind, although, as I hope to show, it is capable of disproof.

Only animals of the same species, or of closely related species, can breed together. Closely allied animals are alike in all respects, except as regards the slight differences which distinguish species, varieties and individuals from each other. Since no animals or plants can cross except those which have most of their past history in common, and which are therefore alike in nearly every respect, it is plainly impossible to prove, from the phenomena of crossing, that each parent has power to transmit the features which are shared by the other parent as well. The phenomena of parthenogenesis, or reproduction by virgin females, as in the case of bees and wasps, show that the ovum alone may transmit all the established hereditary structure of the species, but there is and can be no evidence to show that the male element can accomplish the same thing.

The facts of crossing, while they cannot prove that the

functions of the two reproductive elements are alike, do furnish convincing proof of the contrary, and show that they are not alike.

A reciprocal cross is a double cross between two species or varieties, one form being used in one case as the father, and in the other case as the mother. Thus a reciprocal cross between a horse and an ass is a double cross, between the male horse and the female ass on the one hand, and the female horse and male ass on the other.

Now, if it is true that the function of the ovum is like that of the male cell, the offspring of reciprocal crosses should be alike in all respects, but this is by no means the case.

In the first place, the degree of sterility often differs greatly in two species when reciprocally crossed; for the male of the first will, in some cases, readily fertilize the ovum of the second, and thus give rise to descendants; while hundreds of attempts to fertilize the ovum of the first by the male of the second, result in uniform failure. It often happens also that even when both crosses result in the production of offspring, the hybrid in the one case is sterile, while in the other case it is perfectly fertile.

Not only do the results of reciprocal crossing show this difference, but they show what is still less reconcilable with the view that the functions of the sexual elements are alike, namely, great differences of structure.

In some cases where a reciprocal cross is perfectly fertile on both sides, the hybrids which are thus produced are not at all alike. When the male of species A and the female of B are crossed, the offspring is an entirely different being from the one born from A as a mother with B as a father.

We know that allied species of animals are the descend-

ants of a common ancestral form, from which they inherit all that they have in common, while the distinctive peculiarities which distinguish them from each other are more recently acquired.

According to our hypothesis the ovum transmits established characteristics, while the cells which have recently varied in the body of the male transmit gemmules.

If, then, we select two allied species or varieties and cross the male of one with the female of the other, and then, reversing the process, cross the female of the first form with the male of the second, we should expect to find, in many cases, a difference in the offspring. Where the male of species or variety A is crossed with the female of B, the offspring will inherit from its mother the common characteristics of both parents, and it will also receive from its father gemmules from those cells which have recently varied in the species A. The corresponding cells of its body will therefore be hybrids, and will bear a closer resemblance than the other parts of its body to the species A. That is, the hybrid will share, to some extent, the peculiarities which are distinctive of the species A as compared with B. The offspring of the opposite cross will, on the other hand, join, more or less perfectly, to the common race characteristics, some of the distinctive peculiarities of the species A produced in it by the hybridization of the cells of its body by gemmules received from its father.

Reciprocal crosses between the horse and the ass have been reared for domestic purposes for ages, and Huxley gives the following interesting account of the result:

“The offspring of the ass and the horse, or rather of the he-ass and the mare, is what is called a mule; and, on the other hand, the offspring of the stallion and the

she-ass is what is called a hinney. It is a very rare thing in this country to see a hinney. I never saw one myself; but they have been very carefully studied. Now the curious thing is this, that although you have the same elements in the experiment in each case, the offspring is entirely different in character, according as the male influence comes from the ass or the horse. When the ass is used as the male, as in the case of the mule, you find that the head is like that of the ass, that the ears are long, the tail is tufted at the end, the feet are small, and the voice is an unmistakable bray; these are all points of similarity to the ass; but, on the other hand, the barrel of the body and the cut of the neck are much more like those of the mare. Then if you look at the hinney—the result of the union of the stallion and the she-ass—then you find it is the horse which has the predominance; that the head is more like that of the horse; the ears are shorter, the legs coarser, and the type is altogether altered, while the voice, instead of being a bray, is the ordinary neigh of the horse. Here, you see, is a most curious thing; you take exactly the same elements, ass and horse, but you combine the sexes in a different manner, and the result is modified accordingly.”

It would certainly be a wonderful thing if the combination of the same elements should give such different results, and I think we must conclude that the elements are not the same, but that the ovum and the male cell do not play the same parts in heredity.

There are not many cases in which reciprocal crosses have been made so frequently, and single observations are not of very great value. I will, however, cite a few, to show that the one given is not exceptional. The Manx cat is a variety of the domestic cat peculiar to the Isle of Man. It differs from the ordinary cat in having no tail,

and in some other slight peculiarities; its hind legs are longer, and its habits peculiar. According to Mr. Orton (*Physiology of Breeding*, 1855, p. 9; quoted by Darwin, *Variation*, ii. 86), Dr. Wilson crossed a male Manx cat with common cats, and, out of twenty-three kittens, seventeen were destitute of tails; but when the female Manx was crossed by common male cats all the kittens had tails, though they were generally short and imperfect. Darwin gives the following in his *Variation under Domestication* (ii. 85): "Godina has given a curious case of a ram of a goat-like breed of sheep from the Cape of Good Hope, which produced offspring hardly to be distinguished from himself when crossed with ewes of twelve other breeds. But two of these half-bred ewes, when put to a merino ram, produced lambs closely resembling the merino breed."

I quote the following from Darwin also (p. 87): "The silk fowl breeds true, and there is reason to believe that it is a very ancient race; but when I reared a large number of mongrels from a silk hen by a Spanish cock, not one exhibited even a trace of the so-called silkiness. Mr. Hewitt also asserts that in no instance are the silky feathers transmitted by this breed when crossed with any other variety. But three birds out of many raised by Mr. Orton from a cross between a silk cock and a bantam hen had silky feathers.

There are some instances of reciprocal crosses which seem at first sight to give directly opposite results, and therefore to contradict our theory.

Thus Darwin says that a hybrid which had for its mother a bay mare and for its father a hybrid between a male ass and a female zebra, had, when young, zebra-like stripes upon its shoulders, flanks and legs. Here the only recent striped ancestor is the paternal grand-

mother. As the possession of stripes is a characteristic which distinguishes the zebra from the horse and the ass, it seems at first as if its transmission by a female ancestor is opposed to our theory. We know, however, that all the species of the horse genus are the descendants of a striped form, and the presence of stripes in the zebra is not due to recent variation, but to the fact that it has not varied. The transmission of stripes by a female zebra is therefore nothing more than we might expect. We know, too, that both the horse and the ass show a tendency to revert to the striped ancestral form, and I shall show in the next section that reversion is often excited by crossing. It is therefore quite probable that the stripes in this colt were due to reversion.

It is said that young animals born from a tigress by a male lion, as well as those born from a lioness by a male tiger, are striped, but many cat-like animals show a tendency to revert to a striped form, and in this case also we may explain the presence of stripes in the young by attributing it to reversion excited by crossing.

Darwin says that a good authority assures him that in South America, when niata cattle are crossed with common cattle, though the niata is prepotent whether males or females are used, the prepotency is strongest through the female line.

The origin of the niata breed is not known, but there is no doubt that it originated in Paraguay from common cattle; and the fact that the niata peculiarities are not shared by any other living cattle, but are very much like those of the extinct *Sivatherium*, seems to show that in this case also the peculiarity may be due to reversion to some remote ancestral form.

Difficulty of Explaining the Transmission of the Characters of Two Forms without Fusion.

A much more serious difficulty is found in the fact that while a hybrid is usually somewhat intermediate between its parents, it occasionally happens that the characteristics of one or both parents refuse to blend and are transmitted in an unmodified state. Thus Darwin states that when gray and white mice are paired the young are not piebald nor of an intermediate tint, but are pure white or of the ordinary gray color. This particular case may perhaps be explained as follows: The brown form is the ancestral form, and when no hair gemmules are transmitted the young are brown. All the hairs are homologous with each other, and are derived from the same part of the egg, and when gemmules are transmitted they may hybridize alike all the cells which are to form hairs, and the hybrid animals will therefore be entirely white or entirely brown.

It is stated that when a black game fowl is crossed with a white, the young are either pure black or pure white. but this case is precisely like that of the mice.

Darwin gives a number of interesting illustrations of this singular phenomenon, among which are the following:

When turnspit dogs and ancon sheep, both of which have dwarfed limbs, are crossed with common breeds, the offspring are not intermediate in structure, but resemble one parent only.

When tailless or hornless animals are crossed with perfect animals, it frequently but by no means invariably happens that the offspring are either perfectly furnished with these organs or are quite destitute of them.

When Dorking fowls with five toes are crossed with

other breeds, the chickens often have five toes on one foot and four on the other.

When the red flowered stock of *Antirrhinum* is fertilized with the pollen of the purple Queen stock, about half the seedlings resemble the mother plant, while the other half bear rich purple blossoms like those of the paternal plant.

Darwin says that he fertilized the purple sweet-pea, which has a dark reddish-purple standard-petal and violet-colored wings and keel, with pollen of the painted-lady sweet-pea, which has a pale cherry-colored standard and almost white wings and keel, and from the same pod twice raised plants resembling both sorts, the greater number resembling the father.

These cases are difficult to explain, but the phenomena are so complicated that it is hardly safe to speculate upon them until they are re-examined by an observer who can devote himself to this subject especially.

Some of them may be due to the causes above indicated, and some, possibly, to fertilization by two fathers.

Crossing as a Cause of Reversion.

According to Darwin's view reversion must in all cases be due to the manifestation of a tendency which has lain dormant in the egg and has been transmitted for generations in a latent condition, for the chances against the repetition, by an accidental variation, of a characteristic of a remote ancestor, are inconceivably great.

According to our theory this is not the case, for the conditions which caused a cell in the ancestral form to throw off gemmules and thus to produce a given peculiarity may cause the corresponding cell of the parent to throw off gemmules in the same way, and these, uniting with the corresponding part of the egg, will produce

variation. As the gemmule and the ovarian element are both very similar to those which produced the variation in the ancestor, the chances are not very great against the reproduction of the same peculiarity. In this case we should have a new variation with all the characteristics of a true reversion, but due to the transmission of a gemmule, rather than to the sudden awakening of a tendency which has long lain dormant in the egg.

It is possible, therefore, that there may be two kinds of reversion—true hereditary reappearance of features which have lain latent in the egg, and new variations which repeat again certain old characteristics of the race. There are, I think, certain reasons for believing that reversions of the latter kind are the most common, the chief one being the fact that most of the causes of variability are also causes of reversion.

Thus, crossing, which is a very efficient cause of variation, is also one of the chief causes of reversion.

Darwin gives a number of examples to show that, independently of the well-known tendency of hybrids and mongrels to revert, after a number of generations, to one of the parent forms, the act of crossing in itself gives an impulse towards reversion, and often results in the reappearance of long-lost characters.

The following interesting account, from Darwin's *Variation* (Vol. ii. p. 57), will serve to illustrate this law:

“In the chapter on the horse, reasons were assigned for believing that the primitive stock was striped and dun colored, and details were given showing that in all parts of the world stripes of a dark color frequently appear along the spine, across the legs and on the shoulders, where they are occasionally double or treble, and even sometimes on the face and body of horses of all breeds and of all colors. But the stripes appear most

frequently on the various kinds of dun. They may sometimes plainly be seen on foals and subsequently disappear.

“The dun color and the stripes are strongly transmitted when a horse thus characterized is crossed with any other, but I was not able to prove that striped duns are generally produced from the crossing of two distinct breeds, neither of which are duns, although this does sometimes occur.

“The legs of the ass are often striped, and this may be considered as a reversion to the wild parent form, the *Asinus tæniopus* of Abyssinia, which is thus striped. In the domestic animal the stripes on the shoulder are occasionally double or forked at the extremity, as in certain zebnine species. There is reason to believe that the foal is frequently more plainly striped on the legs than the adult animal. As with the horse, I have not acquired any distinct evidence that the crossing of differently colored varieties of the ass brings out the stripes.

“But now let us turn to the result of crossing the horse and ass. Although mules are not nearly so numerous in England as asses, I have seen a much greater number with striped legs, and with the stripes far more conspicuous than in either parent form. Such mules are generally light-colored, and might be called fallow-duns. The shoulder stripe in one instance was deeply forked at the extremity, and in another instance was double, though united in the middle. Mr. Martin gives a figure of a Spanish mule with strong zebra-like marks on its legs, and remarks that mules are particularly liable to be thus striped on the legs. In South America, according to Roulin, such stripes are more frequent and conspicuous in the mule than in the ass. In the United States, Mr. Gosse, speaking of these animals, says that in a great

number, perhaps in nine out of every ten, the legs are banded with transverse dark stripes."

Mules with striped legs can be seen in great numbers every day in the streets of Baltimore, and the peculiarity is not in the least uncommon.

Darwin gives a number of cases in which the same reversion has been produced by the crossing of other horse-like forms, and we must regard the tendency to revert to a striped form when crossed as characteristic of the horse family.

Darwin says that when he crossed different varieties of fowls he often got birds with faint traces of the peculiar red plumage of the wild *Gallus bankiva*, and that this plumage was almost perfectly reproduced in one magnificent bird, the offspring of a black Spanish cock and a white silk hen, although either of these pure breeds may be reared by tens of thousands without the appearance of a single red feather.

Even long-lost instincts may be made to reappear by crossing. The original wild ancestor of our domestic fowls must, like all wild incubating birds, have had the incubating instinct. Now when two non-sitting breeds of fowls are crossed, the mongrels frequently recover their incubating habit and sit with remarkable steadiness.

It is said that hybrids between perfectly tame domestic animals are often as wild as their wild ancestors. This has been noticed in cattle, pigs, fowls, ducks, and it is probable that the same thing frequently shows itself when widely separated human races are crossed, as such good authorities as Livingston and Humboldt have remarked upon the savage character of half-caste human beings.

Another interesting resemblance between reversion and

ordinary variation is the fact that the descendants of hybrids are more apt to revert than the hybrids themselves. Darwin says (*Variation*, p. 65) that this is a general rule.

Now, whether reversion be due to the sudden excitement of a tendency which has long been transmitted in a dormant state by the ova, or whether it is due to the appearance of a new variation which resembles an old one, we can readily understand how, according to our theory of heredity, crossing should call this power into action. During the evolution of the species each hereditary peculiarity has been established in the egg by gemmules, and anything which prevents the egg from following its normal course and developing the recently acquired characteristics of the species, would allow older characteristics to appear in their place.

We know that animals which are very widely separated are infertile, and we can understand that even when the difference between two species is not great enough to prevent them from crossing, those cells of their bodies which have varied most may be so different from each other that gemmules from the one cannot fertilize the egg-particles which are to produce the other, or when they do fertilize them they may give rise to a variation which is so different from the normal cell that it cannot live. The cells which precede these in the order of growth being less different in the two parents, would be much more favorably situated, and would thus give to the embryo a characteristic of longer standing than the peculiarities of either parent. On the other hand, if reversion is simply variation, we can see that crossing might excite reversion just as it excites variability.

Summary of Chapter.

The study of hybrids gives us a means of comparing, within certain narrow limits, the parts which the two sexual elements play in heredity. The influence of each sex can, in a certain sense, be studied by itself when a given species is used in the one case as the father of a hybrid, and in another case as the mother. The value of crossing as an experiment in heredity is greatly limited, however, by the fact that, although we can study the influence of one sexual element unobscured by the other element from the same species, it is obscured and complicated by the influence of this element from an allied species, and in all organisms which can breed together the reproductive elements must be essentially alike.

Hybrids do, however, present a number of peculiarities which agree perfectly with what we should expect according to our hypothesis, and certain of these are inexplicable without it.

Hybrids and mongrels are highly variable, as we should expect to be the case, according to Darwin's pangenesis hypothesis. This hypothesis fails to account for the fact that hybrids from forms which have long been domesticated are more variable than those from wild species or varieties, or for the very remarkable fact that the children of hybrids are much more variable than the hybrids themselves.

Our theory not only explains the variability of hybrids, but it also accounts for the two latter peculiarities, for crossing will not give rise to a marked or conspicuous variation unless the hybrid inherits numbers of gemmules, and as domesticated animals and plants live under unnatural conditions they are more favorably placed than wild forms for the production of gemmules.

The body of a hybrid is in itself a new thing, and therefore in a certain sense unnatural, and a male hybrid is, accordingly, more fitted for the production of gemmules than a male of a pure or unmixed race.

When a male hybrid is crossed with the female of either pure species or with a third species, the children are much more variable than those born from a hybrid mother by a male of a pure species. It would be difficult to devise an experiment better fitted than this to show that variation is caused by the influence of the male, and that the action of unnatural or changed conditions upon the male parent results in the variability of the child.

The remarkable history of reciprocal hybrids is directly opposed to Darwin's view that the functions of the two reproductive elements are essentially similar, for in some cases it is impossible to breed from a female of one species by the male of a second species, while the male of the first species readily fertilizes the ovum of the second and gives rise to fertile offspring. Even when both crosses are fertile the one is often much more so than the other.

The hybrids of one cross often differ remarkably from those of the other cross in general structure, and in many cases they show, in addition to the common characteristics of both parents, a tendency, more or less perfectly pronounced, to develop the recently acquired characteristics of that species which is used as the father.

This law is often obscured by the appearance of reversions, which are peculiarly apt to occur in hybrids, and by the presence, in certain cases, of a tendency for each parent to transmit its peculiarities to the hybrid, without fusion with those of the other parent. But when we

consider the great obscurity and complexity of the case, and the great difficulty in conducting rigid experiments, the balance of the evidence from hybrids seems to be greatly in favor of our view of the nature of heredity. It certainly presents features which are inexplicable in any other way, and perfectly simple and natural if our view is accepted.