CHAPTER XIX.

SUMMARY OF THE FOUR LAST CHAPTERS, WITH REMARKS ON HYBRIDISM.

ON THE EFFECTS OF CROSSING—THE INFLUENCE OF DOMESTICATION ON FERTILITY—CLOSE INTERBREEDING—GOOD AND EVIL RESULTS FROM CHANGED CONDITIONS OF LIFE—VARIETIES WHEN CROSSED NOT INVARIABLY FERTILE—ON THE DIFFERENCE IN FERTILITY BETWEEN CROSSED SPECIES AND VARIETIES—CONCLUSIONS WITH RESPECT TO HYBRIDISM—LIGHT THROWN ON HYBRIDISM BY THE ILLEGITIMATE PROGENY OF HETEROSTYLED PLANTS—STERILITY OF CROSSED SPECIES DUE TO DIFFERENCES CONFINED TO THE REPRODUCTIVE SYSTEM—NOT ACCUMULATED THROUGH NATURAL SELECTION—REASONS WHY DOMESTIC VARIETIES ARE NOT MUTUALLY STERILE—TOO MUCH STRESS HAS BEEN LAID ON THE DIFFERENCE IN FERTILITY BETWEEN CROSSED SPECIES AND CROSSED VARIETIES—CONCLUSION.

IT was shown in the fifteenth chapter that when individuals of the same variety, or even of a distinct variety, are allowed freely to intercross, uniformity of character is ultimately acquired. Some few characters, however, are incapable of fusion, but these are unimportant, as they are often of a semi-monstrous nature, and have suddenly appeared. Hence, to preserve our domesticated breeds true, or to improve them by methodical selection, it is obviously necessary that they should be kept separate. Nevertheless, a whole body of individuals may be slowly modified, through unconscious selection, as we shall see in a future chapter, without separating them into distinct lots. Domestic races have often been intentionally modified by one or two crosses, made with some allied race, and occasionally even by repeated crosses with very distinct races; but in almost all such cases, long-continued and careful selection has been absolutely necessary, owing to the excessive variability of the crossed offspring, due to the principle of reversion. In a few instances, however, mongrels have retained a uniform character from their first production.

When two varieties are allowed to cross freely, and one is

much more numerous than the other, the former will ultimately absorb the latter. Should both varieties exist in nearly equal numbers, it is probable that a considerable period would elapse before the acquirement of a uniform character; and the character ultimately acquired would largely depend on prepotency of transmission and on the conditions of life; for the nature of these conditions would generally favour one variety more than another, so that a kind of natural selection would come into play. Unless the crossed offspring were slaughtered by man without the least discrimination, some degree of unmethodical selection would likewise come into action. From these several considerations we may infer, that when two or more closely allied species first came into the possession of the same tribe, their crossing will not have influenced, in so great a degree as has often been supposed, the character of the offspring in future times; although in some cases it probably has had a considerable effect.

Domestication, as a general rule, increases the prolificness of animals and plants. It eliminates the tendency to sterility which is common to species when first taken from a state of nature and crossed. On this latter head we have no direct evidence; but as our races of dogs, cattle, pigs, &c., are almost certainly descended from aboriginally distinct stocks, and as these races are now fully fertile together, or at least incomparably more fertile than most species when crossed, we may with entire confidence accept this conclusion.

Abundant evidence has been given that crossing adds to the size, vigour, and fertility of the offspring. This holds good when there has been no previous close interbreeding. It applies to the individuals of the same variety but belonging to different families, to distinct varieties, sub-species, and even to species. In the latter case, though size is gained, fertility is lost; but the increased size, vigour, and hardiness of many hybrids cannot be accounted for solely on the principle of compensation from the inaction of the reproductive system. Certain plants whilst growing under their natural conditions, others when cultivated, and others of hybrid origin, are completely self-impotent, though per-

fectly healthy; and such plants can be stimulated to fertility only by being crossed with other individuals of the same or of a distinct species.

On the other hand, long-continued close interbreeding between the nearest relations diminishes the constitutional vigour, size, and fertility of the offspring; and occasionally leads to malformations, but not necessarily to general deterioration of form or structure. This failure of fertility shows that the evil results of interbreeding are independent of the augmentation of morbid tendencies common to both parents, though this augmentation no doubt is often highly injurious. Our belief that evil follows from close interbreeding rests to a certain extent on the experience of practical breeders, especially of those who have reared many animals of quickly propagating kinds; but it likewise rests on several carefully recorded experiments. With some animals close interbreeding may be carried on for a long period with impunity by the selection of the most vigorous and healthy individuals; but sooner or later evil follows. The evil, however, comes on so slowly and gradually that it easily escapes observation, but can be recognised by the almost instantaneous manner in which size, constitutional vigour, and fertility are regained when animals that have long been interbred are crossed with a distinct family.

These two great classes of facts, namely, the good derived from crossing, and the evil from close interbreeding, with the consideration of the innumerable adaptations throughout nature for compelling, or favouring, or at least permitting, the occasional union of distinct individuals, taken together, lead to the conclusion that it is a law of nature that organic beings shall not fertilise themselves for perpetuity. This law was first plainly hinted at in 1799, with respect to plants, by Andrew Knight,[1] and, not long afterwards, that sagacious

[1] 'Transactions Phil. Soc.,' 1799, p. 202. For Kölreuter, *see* 'Mém. de l'Acad. de St.-Pétersbourg,' tom. iii. 1809 (published 1811), p. 197. In reading C. K. Sprengel's remarkable work, 'Das entdeckte Geheimniss,' &c., 1793, it is curious to observe how often this wonderfully acute observer failed to understand the full meaning of the structure of the flowers which he has so well described, from not always having before his mind the key to the problem, namely, the good derived from the crossing of distinct individual plants.

observer Kölreuter, after showing how well the Malvaceæ are adapted for crossing, asks, "an id aliquid in recessu habeat, quod hujuscemodi flores nunquam proprio suo pulvere, sed semper eo aliarum suæ speciei impregnentur, merito quæritur? Certe natura nil facit frustra." Although we may demur to Kölreuter's saying that nature does nothing in vain, seeing how many rudimentary and useless organs there are, yet undoubtedly the argument from the innumerable contrivances, which favour crossing, is of the greatest weight. The most important result of this law is that it leads to uniformity of character in the individuals of the same species. In the case of certain hermaphrodites, which probably intercross only at long intervals of time, and with unisexual animals inhabiting somewhat separated localities, which can only occasionally come into contact and pair, the greater vigour and fertility of the crossed offspring will ultimately tend to give uniformity of character. But when we go beyond the limits of the same species, free intercrossing is barred by the law of sterility.

In searching for facts which might throw light on the cause of the good effects from crossing, and of the evil effects from close interbreeding, we have seen that, on the one hand, it is a widely prevalent and ancient belief, that animals and plants profit from slight changes in their condition of life; and it would appear that the germ, in a somewhat analogous manner, is more effectually stimulated by the male element, when taken from a distinct individual, and therefore slightly modified in nature, than when taken from a male having the same identical constitution. On the other hand, numerous facts have been given, showing that when animals are first subjected to captivity, even in their native land, and although allowed much liberty, their reproductive functions are often greatly impaired or quite annulled. Some groups of animals are more affected than others, but with apparently capricious exceptions in every group. Some animals never or rarely couple under confinement; some couple freely, but never or rarely conceive. The secondary male characters, the maternal functions and instincts, are occasionally affected. With plants, when first subjected to cultivation, analogous facts

have been observed. We probably owe our double flowers, rich seedless fruits, and in some cases greatly developed tubers, &c., to incipient sterility of the above nature combined with a copious supply of nutriment. Animals which have long been domesticated, and plants which have long been cultivated, can generally withstand, with unimpaired fertility, great changes in their conditions of life; though both are sometimes slightly affected. With animals the somewhat rare capacity of breeding freely under confinement, together with their utility, mainly determine the kinds which have been domesticated.

We can in no case precisely say what is the cause of the diminished fertility of an animal when first captured, or of a plant when first cultivated; we can only infer that it is caused by a change of some kind in the natural conditions of life. The remarkable susceptibility of the reproductive system to such changes,—a susceptibility not common to any other organ,—apparently has an important bearing on Variability, as we shall see in a future chapter.

It is impossible not to be struck with the double parallelism between the two classes of facts just alluded to. On the one hand, slight changes in the conditions of life, and crosses between slightly modified forms or varieties, are beneficial as far as prolificness and constitutional vigour are concerned. On the other hand, changes in the conditions greater in degree, or of a different nature, and crosses between forms which have been slowly and greatly modified by natural means,—in other words, between species,—are highly injurious, as far as the reproductive system is concerned, and in some few instances as far as constitutional vigour is concerned. Can this parallelism be accidental? Does it not rather indicate some real bond of connection? As a fire goes out unless it be stirred up, so the vital forces are always tending, according to Mr. Herbert Spencer, to a state of equilibrium, unless disturbed and renovated through the action of other forces.

In some few cases varieties tend to keep distinct, by breeding at different seasons, by great difference in size, or by sexual preference. But the crossing of varieties, far from

diminishing, generally adds to the fertility of the first union and of the mongrel offspring. Whether all the more widely distinct domestic varieties are invariably quite fertile when crossed, we do not positively know; much time and trouble would be requisite for the necessary experiments, and many difficulties occur, such as the descent of the various races from aboriginally distinct species, and the doubts whether certain forms ought to be ranked as species or varieties. Nevertheless, the wide experience of practical breeders proves that the great majority of varieties, even if some should hereafter prove not to be indefinitely fertile *inter se*, are far more fertile when crossed, than the vast majority of closely allied natural species. A few remarkable cases have, however, been given on the authority of excellent observers, showing that with plants certain forms, which undoubtedly must be ranked as varieties, yield fewer seeds when crossed than is natural to the parent-species. Other varieties have had their reproductive powers so far modified that they are either more or less fertile than their parents, when crossed with a distinct species.

Nevertheless, the fact remains indisputable that domesticated varieties, of animals and of plants, which differ greatly from one another in structure, but which are certainly descended from the same aboriginal species, such as the races of the fowl, pigeon, many vegetables, and a host of other productions, are extremely fertile when crossed; and this seems to make a broad and impassable barrier between domestic varieties and natural species. But, as I will now attempt to show, the distinction is not so great and overwhelmingly important as it at first appears.

On the Difference in Fertility between Varieties and Species when crossed.

This work is not the proper place for fully treating the subject of hybridism, and I have already given in my 'Origin of Species' a moderately full abstract. I will here merely enumerate the general conclusions which may be relied on, and which bear on our present point.

Firstly, the laws governing the production of hybrids are

identical, or nearly identical, in the animal and vegetable kingdoms.

Secondly, the sterility of distinct species when first united, and that of their hybrid offspring, graduate, by an almost infinite number of steps, from zero, when the ovule is never impregnated and a seed-capsule is never formed, up to complete fertility. We can only escape the conclusion that some species are fully fertile when crossed, by determining to designate as varieties all the forms which are quite fertile. This high degree of fertility is, however, rare. Nevertheless, plants, which have been exposed to unnatural conditions, sometimes become modified in so peculiar a manner, that they are much more fertile when crossed with a distinct species than when fertilised by their own pollen. Success in effecting a first union between two species, and the fertility of their hybrids, depend in an eminent degree on the conditions of life being favourable. The innate sterility of hybrids of the same parentage and raised from the same seed-capsule often differs much in degree.

Thirdly, the degree of sterility of a first cross between two species does not always run strictly parallel with that of their hybrid offspring. Many cases are known of species which can be crossed with ease, but yield hybrids excessively sterile; and conversely some which can be crossed with great difficulty, but produce fairly fertile hybrids. This is an inexplicable fact, on the view that species have been specially endowed with mutual sterility in order to keep them distinct.

Fourthly, the degree of sterility often differs greatly in two species when reciprocally crossed; for the first will readily fertilise the second; but the latter is incapable, after hundreds of trials, of fertilising the former. Hybrids produced from reciprocal crosses between the same two species likewise sometimes differ in their degree of sterility. These cases also are utterly inexplicable on the view of sterility being a special endowment.

Fifthly, the degree of sterility of first crosses and of hybrids runs, to a certain extent, parallel with the general or systematic affinity of the forms which are united. For species be-

longing to distinct genera can rarely, and those belonging to distinct families can never, be crossed. The parallelism, however, is far from complete; for a multitude of closely allied species will not unite, or unite with extreme difficulty, whilst other species, widely different from one another, can be crossed with perfect facility. Nor does the difficulty depend on ordinary constitutional differences, for annual and perennial plants, deciduous and evergreen trees, plants flowering at different seasons, inhabiting different stations, and naturally living under the most opposite climates, can often be crossed with ease. The difficulty or facility apparently depends exclusively on the sexual constitution of the species which are crossed; or on their sexual elective affinity, *i.e. Wahlverwandtschaft* of Gärtner. As species rarely or never become modified in one character, without being at the same time modified in many characters, and as systematic affinity includes all visible similarities and dissimilarities, any difference in sexual constitution between two species would naturally stand in more or less close relation with their systematic position.

Sixthly, the sterility of species when first crossed, and that of hybrids, may possibly depend to a certain extent on distinct causes. With pure species the reproductive organs are in a perfect condition, whilst with hybrids they are often plainly deteriorated. A hybrid embryo which partakes of the constitution of its father and mother is exposed to unnatural conditions, as long as it is nourished within the womb, or egg, or seed of the mother-form; and as we know that unnatural conditions often induce sterility, the reproductive organs of the hybrid might at this early age be permanently affected. But this cause has no bearing on the infertility of first unions. The diminished number of the offspring from first unions may often result, as is certainly sometimes the case, from the premature death of most of the hybrid embryos. But we shall immediately see that a law of an unknown nature apparently exists, which leads to the offspring from unions, which are infertile, being themselves more or less infertile; and this at present is all that can be said.

Seventhly, hybrids and mongrels present, with the one great

exception of fertility, the most striking accordance in all other respects; namely, in the laws of their resemblance to their two parents, in their tendency to reversion, in their variability, and in being absorbed through repeated crosses by either parent-form.

After arriving at these conclusions, I was led to investigate a subject which throws considerable light on hybridism, namely, the fertility of heterostyled or dimorphic and trimorphic plants, when illegitimately united. I have had occasion several times to allude to these plants, and I may here give a brief abstract of my observations. Several plants belonging to distinct orders present two forms, which exist in about equal numbers, and which differ in no respect except in their reproductive organs; one form having a long pistil with short stamens, the other a short pistil with long stamens; both with differently sized pollen-grains. With trimorphic plants there are three forms likewise differing in the lengths of their pistils and stamens, in the size and colour of the pollen-grains, and in some other respects; and as in each of the three forms there are two sets of stamens, there are altogether six sets of stamens and three kinds of pistils. These organs are so proportioned in length to one another that, in any two of the forms, half the stamens in each stand on a level with the stigma of the third form. Now I have shown, and the result has been confirmed by other observers, that, in order to obtain full fertility with these plants, it is necessary that the stigma of the one form should be fertilised by pollen taken from the stamens of corresponding height in the other form. So that with dimorphic species two unions, which may be called legitimate, are fully fertile, and two, which may be called illegitimate, are more or less infertile. With trimorphic species six unions are legitimate, or fully fertile, and twelve are illegitimate, or more or less infertile.[2]

The infertility which may be observed in various dimorphic

[2] My observations 'On the Character and hybrid-like nature of the offspring from the illegitimate union of Dimorphic and Trimorphic Plants' were published in the 'Journal of the Linnean Soc.,' vol. x. p. 393. The abstract here given is nearly the same with that which appeared in the 6th edition of my 'Origin of Species.'

and trimorphic plants, when illegitimately fertilised, that is, by pollen taken from stamens not corresponding in height with the pistil, differs much in degree, up to absolute and utter sterility; just in the same manner as occurs in crossing distinct species. As the degree of sterility in the latter case depends in an eminent degree on the conditions of life being more or less favourable, so I have found it with illegitimate unions. It is well known that if pollen of a distinct species be placed on the stigma of a flower, and its own pollen be afterwards, even after a considerable interval of time, placed on the same stigma, its action is so strongly prepotent that it generally annihilates the effect of the foreign pollen; so it is with the pollen of the several forms of the same species, for legitimate pollen is strongly prepotent over illegitimate pollen, when both are placed on the same stigma. I ascertained this by fertilising several flowers, first illegitimately, and twenty-four hours afterwards legitimately, with pollen taken from a peculiarly coloured variety, and all the seedlings were similarly coloured; this shows that the legitimate pollen, though applied twenty-four hours subsequently, had wholly destroyed or prevented the action of the previously applied illegitimate pollen. Again, as, in making reciprocal crosses between the same two species, there is occasionally a great difference in the result, so the same thing occurs with trimorphic plants; for instance, the mid-styled form of *Lythrum salicaria* could be illegitimately fertilised with the greatest ease by pollen from the longer stamens of the short-styled form, and yielded many seeds; but the short-styled form did not yield a single seed when fertilised by the longer stamens of the mid-styled form.

In all these respects the forms of the same undoubted species, when illegitimately united, behave in exactly the same manner as do two distinct species when crossed. This led me carefully to observe during four years many seedlings, raised from several illegitimate unions. The chief result is that these illegitimate plants, as they may be called, are not fully fertile. It is possible to raise from dimorphic species, both long-styled and short-styled illegitimate plants, and from trimorphic plants all three illegitimate forms. These

can then be properly united in a legitimate manner. When this is done, there is no apparent reason why they should not yield as many seeds as did their parents when legitimately fertilised. But such is not the case; they are all infertile, but in various degrees; some being so utterly and incurably sterile that they did not yield during four seasons a single seed or even seed-capsule. These illegitimate plants, which are so sterile, although united with each other in a legitimate manner, may be strictly compared with hybrids when crossed *inter se*, and it is well known how sterile these latter generally are. When, on the other hand, a hybrid is crossed with either pure parent-species, the sterility is usually much lessened: and so it is when an illegitimate plant is fertilised by a legitimate plant. In the same manner as the sterility of hybrids does not always run parallel with the difficulty of making the first cross between the two parent-species, so the sterility of certain illegitimate plants was unusually great, whilst the sterility of the union from which they were derived was by no means great. With hybrids raised from the same seed-capsule the degree of sterility is innately variable, so it is in a marked manner with illegitimate plants. Lastly, many hybrids are profuse and persistent flowerers, whilst other and more sterile hybrids produce few flowers, and are weak, miserable dwarfs; exactly similar cases occur with the illegitimate offspring of various dimorphic and trimorphic plants.

Although there is the closest identity in character and behaviour between illegitimate plants and hybrids, it is hardly an exaggeration to maintain that the former are hybrids, but produced within the limits of the same species by the improper union of certain forms, whilst ordinary hybrids are produced from an improper union between so-called distinct species. We have already seen that there is the closest similarity in all respects between first illegitimate unions, and first crosses between distinct species. This will perhaps be made more fully apparent by an illustration: we may suppose that a botanist found two well-marked varieties (and such occur) of the long-styled form of the trimorphic *Lythrum salicaria*, and that he determined to try by crossing

whether they were specifically distinct. He would find that they yielded only about one-fifth of the proper number of seed, and that they behaved in all the other above-specified respects as if they had been two distinct species. But to make the case sure, he would raise plants from his supposed hybridised seed, and he would find that the seedlings were miserably dwarfed and utterly sterile, and that they behaved in all other respects like ordinary hybrids. He might then maintain that he had actually proved, in accordance with the common view, that his two varieties were as good and as distinct species as any in the world; but he would be completely mistaken.

The facts now given on dimorphic and trimorphic plants are important, because they show us, first, that the physiological test of lessened fertility, both in first crosses and in hybrids, is no criterion of specific distinction; secondly, because we may conclude that there is some unknown bond which connects the infertility of illegitimate unions with that of their illegitimate offspring, and we are led to extend the same view to first crosses and hybrids; thirdly, because we find, and this seems to me of especial importance, that two or three forms of the same species may exist and may differ in no respect whatever, either in structure or in constitution, relatively to external conditions, and yet be sterile when united in certain ways. For we must remember that it is the union of the sexual elements of individuals of the same form, for instance, of two long-styled forms, which results in sterility; whilst it is the union of the sexual element proper to two distinct forms which is fertile. Hence the case appears at first sight exactly the reverse of what occurs in the ordinary unions of the individuals of the same species, and with crosses between distinct species. It is, however, doubtful whether this is really so; but I will not enlarge on this obscure subject.

We may, however, infer as probable from the consideration of dimorphic and trimorphic plants, that the sterility of distinct species when crossed, and of their hybrid progeny, depends exclusively on the nature of their sexual elements, and not on any difference in their structure or general con-

stitution. We are also led to this same conclusion by considering reciprocal crosses, in which the male of one species cannot be united, or only with great difficulty, with the female of a second species, whilst the converse cross can be effected with perfect facility. That excellent observer, Gärtner, likewise concluded that species when crossed are sterile owing to differences confined to their reproductive systems.

On the principle which makes it necessary for man, whilst he is selecting and improving his domestic varieties, to keep them separate, it would clearly be advantageous to varieties in a state of nature, that is to incipient species, if they could be kept from blending, either through sexual aversion, or by becoming mutually sterile. Hence it at one time appeared to me probable, as it has to others, that this sterility might have been acquired through natural selection. On this view we must suppose that a shade of lessened fertility first spontaneously appeared, like any other modification, in certain individuals of a species when crossed with other individuals of the same species; and that successive slight degrees of infertility, from being advantageous, were slowly accumulated. This appears all the more probable, if we admit that the structural differences between the forms of dimorphic and trimorphic plants, as the length and curvature of the pistil, &c., have been co-adapted through natural selection; for if this be admitted, we can hardly avoid extending the same conclusion to their mutual infertility. Sterility, moreover, has been acquired through natural selection for other and widely different purposes, as with neuter insects in reference to their social economy. In the case of plants, the flowers on the circumference of the truss in the guelder-rose (*Viburnum opulus*) and those on the summit of the spike in the feather-hyacinth (*Muscari comosum*) have been rendered conspicuous, and apparently in consequence sterile, in order that insects might easily discover and visit the perfect flowers. But when we endeavour to apply the principle of natural selection to the acquirement by distinct species of mutual sterility, we meet with great difficulties. In the first place, it may be remarked that separate regions are often inhabited by groups

of species or by single species, which when brought together and crossed are found to be more or less sterile; now it could clearly have been no advantage to such separated species to have been rendered mutually sterile, and consequently this could not have been effected through natural selection; but it may perhaps be argued, that, if a species were rendered sterile with some one compatriot, sterility with other species would follow as a necessary consequence. In the second place, it is as much opposed to the theory of natural selection, as to the theory of special creation, that in reciprocal crosses the male element of one form should have been rendered utterly impotent on a second form, whilst at the same time the male element of this second form is enabled freely to fertilise the first form; for this peculiar state of the reproductive system could not possibly have been advantageous to either species.

In considering the probability of natural selection having come into action in rendering species mutually sterile, one of the greatest difficulties will be found to lie in the existence of many graduated steps from slightly lessened fertility to absolute sterility. It may be admitted, on the principle above explained, that it would profit an incipient species if it were rendered in some slight degree sterile when crossed with its parent-form or with some other variety; for thus fewer bastardised and deteriorated offspring would be produced to commingle their blood with the new species in process of formation. But he who will take the trouble to reflect on the steps by which this first degree of sterility could be increased through natural selection to that higher degree which is common to so many species, and which is universal with species which have been differentiated to a generic or family rank, will find the subject extraordinarily complex. After mature reflection it seems to me that this could not have been effected through natural selection. Take the case of any two species which, when crossed, produce few and sterile offspring; now, what is there which could favour the survival of those individuals which happened to be endowed in a slightly higher degree with mutual infertility, and which thus approached by one small step towards absolute sterility?

Yet an advance of this kind, if the theory of natural selection be brought to bear, must have incessantly occurred with many species, for a multitude are mutually quite barren. With sterile neuter insects we have reason to believe that modifications in their structure and fertility have been slowly accumulated by natural selection, from an advantage having been thus indirectly given to the community to which they belonged over other communities of the same species; but an individual animal not belonging to a social community, if rendered slightly sterile when crossed with some other variety, would not thus itself gain any advantage or indirectly give any advantage to the other individuals of the same variety, thus leading to their preservation.

But it would be superfluous to discuss this question in detail; for with plants we have conclusive evidence that the sterility of crossed species must be due to some principle, quite independent of natural selection. Both Gärtner and Kölreuter have proved that in general including numerous species, a series can be formed from species which when crossed yield fewer and fewer seeds, to species which never produce a single seed, but yet are affected by the pollen of certain other species, for the germen swells. It is here manifestly impossible to select the more sterile individuals, which have already ceased to yield seeds; so that this acme of sterility, when the germen alone is affected, cannot have been gained through selection; and from the laws governing the various grades of sterility being so uniform throughout the animal and vegetable kingdoms, we may infer that the cause, whatever it may be, is the same or nearly the same in all cases.

As species have not been rendered mutually infertile through the accumulative action of natural selection, and as we may safely conclude, from the previous as well as from other and more general considerations, that they have not been endowed through an act of creation with this quality, we must infer that it has arisen incidentally during their slow formation in connection with other and unknown changes in their organisation. By a quality arising incidentally, I refer to such cases as different species of animals and plants being differently affected by poisons to which they are not naturally

exposed; and this difference in susceptibility is clearly incidental on other and unknown differences in their organisation. So again the capacity in different kinds of trees to be grafted on each other, or on a third species, differs much, and is of no advantage to these trees, but is incidental on structural or functional differences in their woody tissues. We need not feel surprise at sterility incidentally resulting from crosses between distinct species,—the modified descendants of a common progenitor,—when we bear in mind how easily the reproductive system is affected by various causes—often by extremely slight changes in the conditions of life, by too close interbreeding, and by other agencies. It is well to bear in mind such cases as that of the *Passiflora alata*, which recovered its self-fertility from being grafted on a distinct species—the cases of plants which normally or abnormally are self-impotent, but can readily be fertilised by the pollen of a distinct species—and lastly the cases of individual domesticated animals which evince towards each other sexual incompatibility.

We now at last come to the immediate point under discussion: how is it that, with some few exceptions in the case of plants, domesticated varieties, such as those of the dog, fowl, pigeon, several fruit-trees, and culinary vegetables, which differ from each other in external characters more than many species, are perfectly fertile when crossed, or even fertile in excess, whilst closely allied species are almost invariably in some degree sterile? We can, to a certain extent, give a satisfactory answer to this question. Passing over the fact that the amount of external difference between two species is no sure guide to their degree of mutual sterility, so that similar differences in the case of varieties would be no sure guide, we know that with species the cause lies exclusively in differences in their sexual constitution. Now the conditions to which domesticated animals and cultivated plants have been subjected have had so little tendency towards modifying the reproductive system in a manner leading to mutual sterility, that we have very good grounds for admitting the directly opposite doctrine of Pallas, namely, that such conditions

generally eliminate this tendency; so that the domesticated descendants of species, which in their natural state would have been in some degree sterile when crossed, become perfectly fertile together. With plants, so far is cultivation from giving a tendency towards mutual sterility, that in several well-authenticated cases, already often alluded to, certain species have been affected in a very different manner, for they have become self-impotent, whilst still retaining the capacity of fertilising, and being fertilised by, distinct species. If the Pallasian doctrine of the elimination of sterility through long-continued domestication be admitted, and it can hardly be rejected, it becomes in the highest degree improbable that similar circumstances should commonly both induce and eliminate the same tendency; though in certain cases, with species having a peculiar constitution, sterility might occasionally be thus induced. Thus, as I believe, we can understand why with domesticated animals varieties have not been produced which are mutually sterile; and why with plants only a few such cases have been observed, namely, by Gärtner, with certain varieties of maize and verbascum, by other experimentalists with varieties of the gourd and melon, and by Kölreuter with one kind of tobacco.

With respect to varieties which have originated in a state of nature, it is almost hopeless to expect to prove by direct evidence that they have been rendered mutually sterile; for if even a trace of sterility could be detected, such varieties would at once be raised by almost every naturalist to the rank of distinct species. If, for instance, Gärtner's statement were fully confirmed, that the blue and red flowered forms of the pimpernel (*Anagallis arvensis*) are sterile when crossed, I presume that all the botanists who now maintain on various grounds that these two forms are merely fleeting varieties, would at once admit that they were specifically distinct.

The real difficulty in our present subject is not, as it appears to me, why domestic varieties have not become mutually infertile when crossed, but why this has so generally occurred with natural varieties as soon as they have been modified in a sufficient and permanent degree to take rank as species. We are far from precisely knowing the cause; but we can see

that the species, owing to their struggle for existence with numerous competitors, must have been exposed to more uniform conditions of life during long periods of time than domestic varieties have been, and this may well make a wide difference in the result. For we know how commonly wild animals and plants, when taken from their natural conditions and subjected to captivity, are rendered sterile; and the reproductive functions of organic beings which have always lived and been slowly modified under natural conditions would probably in like manner be eminently sensitive to the influence of an unnatural cross. Domesticated productions, on the other hand, which, as shown by the mere fact of their domestication, were not originally highly sensitive to changes in their conditions of life, and which can now generally resist with undiminished fertility repeated changes of conditions, might be expected to produce varieties, which would be little liable to have their reproductive powers injuriously affected by the act of crossing with other varieties which had originated in a like manner.

Certain naturalists have recently laid too great stress, as it appears to me, on the difference in fertility between varieties and species when crossed. Some allied species of trees cannot be grafted on one another, whilst all varieties can be so grafted. Some allied animals are affected in a very different manner by the same poison, but with varieties no such case until recently was known; whilst now it has been proved that immunity from certain poisons sometimes stands in correlation with the colour of the individuals of the same species. The period of gestation generally differs much in distinct species, but with varieties until lately no such difference had been observed. Here we have various physiological differences, and no doubt others could be added, between one species and another of the same genus, which do not occur, or occur with extreme rarity, in the case of varieties; and these differences are apparently wholly or in chief part incidental on other constitutional differences, just in the same manner as the sterility of crossed species is incidental on differences confined to the sexual system. Why, then, should these latter differences, however serviceable they may indirectly be in keeping

the inhabitants of the same country distinct, be thought of such paramount importance, in comparison with other incidental and functional differences? No sufficient answer to this question can be given. Hence the fact that widely distinct domestic varieties are, with rare exceptions, perfectly fertile when crossed, and produce fertile offspring, whilst closely allied species are, with rare exceptions, more or less sterile, is not nearly so formidable an objection as it appears at first to the theory of the common descent of allied species.