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THE VARIATION

OF

ANIMALS AND PLANTS

UNDER DOMESTICATION.

By CHARLES DARWIN, M.A., F.R.S., &c.

IN TWO VOLUMES.—Vol. II.

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ERRATA.

Vol. II., pp. 18, 232, 258, *for* Cratægus oxycantha, *read* oxyacantha.
„ p. 98, 8 lines from top, *for* Dianthus armoria *read* armeria.
„ „ 156, 15 lines from bottom, *for* Casuarinus *read* Casuarius.
„ „ „ 4 lines from bottom, *for* Grus cineria *read* cinerea.
„ „ 168, 11 lines from top, *for* Œsculus *read* Æsculus.
„ „ 300, 3 lines from top, *for* anastomising *read* anastomosing.
„ „ „ foot-note, *for* Birckell *read* Brickell.

THE {1}

VARIATION OF ANIMALS AND PLANTS

UNDER DOMESTICATION.

CHAPTER XII.

INHERITANCE.

WONDERFUL NATURE OF INHERITANCE—PEDIGREES OF OUR DOMESTICATED ANIMALS —INHERITANCE NOT DUE TO CHANCE—TRIFLING CHARACTERS INHERITED—DISEASES INHERITED—PECULIARITIES IN THE EYE INHERITED—DISEASES IN THE HORSE—LONGEVITY AND VIGOUR—ASYMMETRICAL DEVIATIONS OF STRUCTURE—POLYDACTYLISM AND REGROWTH OF SUPERNUMERARY DIGITS AFTER AMPUTATION—CASES OF SEVERAL CHILDREN SIMILARLY AFFECTED FROM NON-AFFECTED PARENTS—WEAK AND FLUCTUATING INHERITANCE: IN WEEPING TREES, IN DWARFNESS, COLOUR OF FRUIT AND FLOWERS, COLOUR OF HORSES—NON-INHERITANCE IN CERTAIN CASES —INHERITANCE OF STRUCTURE AND HABITS OVERBORNE BY HOSTILE CONDITIONS OF LIFE, BY INCESSANTLY RECURRING VARIABILITY, AND BY REVERSION—CONCLUSION.

The subject of inheritance is an immense one, and has been treated by many authors. One work alone, 'De l'Hérédité Naturelle,' by Dr. Prosper Lucas, runs to the length of 1562 pages. We must confine ourselves to certain points which have an important bearing on the general subject of variation, both with domestic and natural productions. It is obvious that a variation which is not inherited throws no light on the derivation of species, nor is of any service to man, except in the case of perennial plants, which can be propagated by buds.

If animals and plants had never been domesticated, and wild ones alone had been observed, we should probably never have heard the saying, that "like begets like." The proposition would have been as self-evident, as that all the buds on the same tree are alike, though neither proposition is strictly true. For, as has often been remarked, probably no two individuals are identically the same. All wild animals recognise each other, which shows {2} that there is some difference between them; and when the eye is well practised, the shepherd

knows each sheep, and man can distinguish a fellow-man out of millions on millions of other men. Some authors have gone so far as to maintain that the production of slight differences is as much a necessary function of the powers of generation, as the production of offspring like their parents. This view, as we shall see in a future chapter, is not theoretically probable, though practically it holds good. The saying that "like begets like" has in fact arisen from the perfect confidence felt by breeders, that a superior or inferior animal will generally reproduce its kind; but this very superiority or inferiority shows that the individual in question has departed slightly from its type.

The whole subject of inheritance is wonderful. When a new character arises, whatever its nature may be, it generally tends to be inherited, at least in a temporary and sometimes in a most persistent manner. What can be more wonderful than that some trifling peculiarity, not primordially attached to the species, should be transmitted through the male or female sexual cells, which are so minute as not to be visible to the naked eye, and afterwards through the incessant changes of a long course of development, undergone either in the womb or in the egg, and ultimately appear in the offspring when mature, or even when quite old, as in the case of certain diseases? Or again, what can be more wonderful than the well-ascertained fact that the minute ovule of a good milking cow will produce a male, from whom a cell, in union with an ovule, will produce a female, and she, when mature, will have large mammary glands, yielding an abundant supply of milk, and even milk of a particular quality? Nevertheless, the real subject of surprise is, as Sir H. Holland has well remarked,[1] not that a character should be inherited, but that any should ever fail to be inherited. In a future chapter, devoted to an hypothesis which I have termed pangenesis, an attempt will be made to show the means by which characters of all kinds are transmitted from generation to generation.

Some writers,[2] who have not attended to natural history, have attempted to show that the {3}
force of inheritance has been much exaggerated. The breeders of animals would smile at such simplicity; and if they condescended to make any answer, might ask what would be the chance of winning a prize if two inferior animals were paired together? They might ask whether the half-wild Arabs were led by theoretical notions to keep pedigrees of their horses? Why have pedigrees been scrupulously kept and published of the Shorthorn cattle, and more recently of the Hereford breed? Is it an illusion that these recently improved animals safely transmit their excellent qualities even when crossed with other breeds? have the Shorthorns, without good reason, been purchased at immense prices and exported to almost every quarter of the globe, a thousand guineas having been given for a bull? With greyhounds pedigrees have likewise been kept, and the names of such dogs, as Snowball, Major, &c., are as well known to coursers as those of Eclipse and Herod on the turf. Even with the Gamecock pedigrees of famous strains were formerly kept, and extended back for a century. With pigs, the Yorkshire and Cumberland breeders "preserve and print pedigrees;" and to show how such highly-bred animals are valued, I may mention that Mr. Brown, who won all the first prizes for small breeds at Birmingham in 1850, sold a young sow and boar of his breed to Lord Ducie for 43 guineas; the sow alone was afterwards sold to the Rev. F. Thursby for 65 guineas; who writes, "she paid me very well, having sold her produce for 300*l*., and having now four breeding sows from her."[3] Hard cash paid down, over and over again, is an excellent test of inherited superiority. In fact, the whole art of breeding, from which such great results have been attained during the present century, depends on the inheritance of each small detail of structure. But inheritance is not certain; for if it were, the {4}
breeder's art[4] would be reduced to a certainty, and there would be little scope left for all that skill and perseverance shown by the men who have left an enduring monument of their success in the present state of our domesticated animals.

It is hardly possible, within a moderate compass, to impress on the mind of those who have not attended to the subject, the full conviction of the force of inheritance which is slowly

acquired by rearing animals, by studying the many treatises which have been published on the various domestic animals, and by conversing with breeders. I will select a few facts of the kind, which, as far as I can judge, have most influenced my own mind. With man and the domestic animals, certain peculiarities have appeared in an individual, at rare intervals, or only once or twice in the history of the world, but have reappeared in several of the children and grandchildren. Thus Lambert, "the porcupine-man," whose skin was thickly covered with warty projections, which were periodically moulted, had all his six children and two grandsons similarly affected.[5] The face and body being covered with long hair, accompanied by deficient teeth (to which I shall hereafter refer), occurred in three successive generations in a Siamese family; but this case is not unique, as a woman[6] with a completely hairy face was exhibited in London in 1663, and another instance has recently occurred. Colonel Hallam[7] has described a race of two-legged pigs, "the hinder extremities being entirely wanting;" and this deficiency was transmitted through three generations. In fact, all races presenting any remarkable peculiarity, such as solid-hoofed swine, Mauchamp sheep, niata cattle, &c., are instances of the long-continued inheritance of rare deviations of structure.

When we reflect that certain extraordinary peculiarities have thus appeared in a single individual out of many millions, all exposed in the same country to the same general conditions of life, and, again, that the same extraordinary peculiarity has sometimes appeared in individuals living under widely different conditions of life, we are driven to conclude that such peculiarities are not directly due to the action of the surrounding conditions, but to unknown laws acting on the organisation or constitution of the individual; —that their production stands in hardly closer relation to the conditions than does life itself. If this be so, and the occurrence of the same unusual character in the child and parent cannot be attributed to both having been exposed to the same unusual conditions, then the following problem is worth consideration, as showing that the result cannot be due, as some authors have supposed, to mere coincidence, but must be consequent on the members of the same family inheriting something in common in their constitution. Let it be assumed that, in a large population, a particular affection occurs on an average in one out of a million, so that the *à priori* chance that an individual taken at random will be so affected is only one in a million. Let the population consist of sixty millions, composed, we will assume, of ten million families, each containing six members. On these data, Professor Stokes has calculated for me that the odds will be no less than 8333 millions to 1 that in the ten million families there will not be even a single family in which one parent and two children will be affected by the peculiarity in question. But numerous cases could be given, in which several children have been affected by the same rare peculiarity with one of their parents; and in this case, more especially if the grandchildren be included in the calculation, the odds against mere coincidence become something prodigious, almost beyond enumeration. {5}

In some respects the evidence of inheritance is more striking when we consider the reappearance of trifling peculiarities. Dr. Hodgkin formerly told me of an English family in which, for many generations, some members had a single lock differently coloured from the rest of the hair. I knew an Irish gentleman, who, on the right side of his head, had a small white lock in the midst of his dark hair: he assured me that his grandmother had a similar lock on the same side, and his mother on the opposite side. But it is superfluous to give instances; every shade of expression, which may often be seen alike in parents and children, tells the same story. On what a curious combination of corporeal structure, mental character, and training, must handwriting depend! yet every one must have noted the occasional close similarity of the handwriting in father and son, although the father had not taught his son. A great collector of franks assured me that in his collection there were several franks of father and son hardly distinguishable except by their dates. Hofacker, in Germany, remarks on the inheritance of handwriting; and it has even been asserted that English boys when taught to write in France naturally cling to their English manner of writing.[8] Gait, gestures, voice, {6}

and general bearing are all inherited, as the illustrious Hunter and Sir A. Carlisle have insisted.[9] My father communicated to me two or three striking instances, in one of which a man died during the early infancy of his son, and my father, who did not see this son until grown up and out of health, declared that it seemed to him as if his old friend had risen from the grave, with all his highly peculiar habits and manners. Peculiar manners pass into tricks, and several instances could be given of their inheritance; as in the case, often quoted, of the father who generally slept on his back, with his right leg crossed over the left, and whose daughter, whilst an infant in the cradle, followed exactly the same habit, though an attempt was made to cure her.[10] I will give one instance which has fallen under my own observation, and which is curious from being a trick associated with a peculiar state of mind, namely, pleasurable emotion. A boy had the singular habit, when pleased, of rapidly moving his fingers parallel to each other, and, when much excited, of raising both hands, with the fingers still moving, to the sides of his face on a level with the eyes; this boy, when almost an old man, could still hardly resist this trick when much pleased, but from its absurdity concealed it. He had eight children. Of these, a girl, when pleased, at the age of {7}
four and a half years, moved her fingers in exactly the same way, and what is still odder, when much excited, the raised both her hands, with her fingers still moving, to the sides of her face, in exactly the same manner as her father had done, and sometimes even still continued to do when alone. I never heard of any one excepting this one man and his little daughter who had this strange habit; and certainly imitation was in this instance out of the question.

Some writers have doubted whether those complex mental attributes, on which genius and talent depend, are inherited, even when both parents are thus endowed. But he who will read Mr. Galton's able paper[11] on hereditary talent will have his doubts allayed.

Unfortunately it matters not, as far as inheritance is concerned, how injurious a quality or structure may be if compatible with life. No one can read the many treatises[12] on hereditary disease and doubt this. The ancients were strongly of this opinion, or, as Ranchin expresses it, *Omnes Græci, Arabes, et Latini in eo consentiunt*. A long catalogue could be given of all sorts of inherited malformations and of predisposition to various diseases. With gout, fifty per cent. of the cases observed in hospital practice are, according to Dr. Garrod, inherited, and a greater percentage in private practice. Every one knows how often insanity runs in families, and some of the cases given by Mr. Sedgwick are awful,—as of a surgeon, whose brother, father, and four paternal uncles were all insane, the latter dying by suicide; of a Jew, whose father, mother, and six brothers and sisters were all mad; and in some other cases several members of the same family, during three or four successive generations, have committed suicide. Striking instances have been recorded of epilepsy, consumption, asthma, {8}
stone in the bladder, cancer, profuse bleeding from the slightest injuries, of the mother not giving milk, and of bad parturition being inherited. In this latter respect I may mention an odd case given by a good observer,[13] in which the fault lay in the offspring, and not in the mother: in a part of Yorkshire the farmers continued to select cattle with large hind-quarters, until they made a strain called "Dutch-buttocked," and "the monstrous size of the buttocks of the calf was frequently fatal to the cow, and numbers of cows were annually lost in calving."

> Instead of giving numerous details on various inherited malformations and diseases, I will confine myself to one organ, that which is the most complex, delicate, and probably best-known in the human frame, namely, the eye, with its accessory parts. To begin with the latter: I have heard of a family in which parents and children were affected by drooping eyelids, in so peculiar a manner, that they could not see without throwing their heads backwards; and Sir A. Carlisle[14] specifies a pendulous fold to the eyelids as inherited. "In a family," says Sir H. Holland,[15] "where the father had a

singular elongation of the upper eyelid, seven or eight children were born with the same deformity; two or three other children having it not." Many persons, as I year from Mr. Paget, have two or three of the hairs in their eyebrows (apparently corresponding with the vibrissæ of the lower animals) much longer than the others; and even so trifling a peculiarity as this certainly runs in families.

With respect to the eye itself, the highest authority in England, Mr. Bowman, has been so kind as to give me the following remarks on certain inherited imperfections. First, hypermetropia, or morbidly long sight: in this affection, the organ, instead of being spherical, is too flat from front to back, and is often altogether too small, so that the retina is brought too forward for the focus of the humours; consequently a convex glass is required for clear vision of near objects, and frequently even of distant ones. This state occurs congenitally, or at a very early age, often in several children of the same family, where one of the parents has presented it.[16] Secondly, myopia, or short-sight, in which the eye is egg-shaped, and too long from front to back; the retina in this case lies behind the focus, and is therefore fitted to see distinctly only very near objects. This condition is not commonly congenital, but comes on in youth, the liability to it being well known to be transmissible from parent to child. The change from the spherical to the ovoidal shape seems the immediate consequence of {9} something like inflammation of the coats, under which they yield, and there is ground for believing that it may often originate in causes acting directly on the individual affected, and may thenceforward become transmissible. When both parents are myopic Mr. Bowman has observed the hereditary tendency in this direction to be heightened, and some of the children to be myopic at an earlier age or in a higher degree than their parents. Thirdly, squinting is a familiar example of hereditary transmission: it is frequently a result of such optical defects as have been above mentioned; but the more primary and uncomplicated forms of it are also sometimes in a marked degree transmitted in a family. Fourthly, *Cataract*, or opacity of the crystalline lens, is commonly observed in persons whose parents have been similarly affected, and often at an earlier age in the children than in the parents. Occasionally more than one child in a family is thus afflicted, one of whose parents or other relation presents the senile form of the complaint. When cataract affects several members of a family in the same generation, it is often seen to commence at about the same age in each; *e.g.*, in one family several infants or young persons may suffer from it; in another, several persons of middle age. Mr. Bowman also informs me that he has occasionally seen, in several members of the same family, various defects in either the right or left eye; and Mr. White Cooper has often seen peculiarities of vision confined to one eye reappearing in the same eye in the offspring.[17]

The following cases are taken from an able paper by Mr. W. Sedgwick, and from Dr. Prosper Lucas.[18] Amaurosis, either congenital or coming on late in life, and causing total blindness, is often inherited; it has been observed in three successive generations. Congenital absence of the iris has likewise been transmitted for three generations, a cleft-iris for four generations, being limited in this latter case to the males of the family. Opacity of the cornea and congenital smallness of the eyes have been inherited. Portal records a curious case, in which a father and two sons were rendered blind, whenever the head was bent downwards, apparently owing to the crystalline lens, with its capsule, slipping through an unusually large pupil into the anterior chamber of the eye. Day-blindness, or imperfect vision under a bright light, is inherited, as is night-blindness, or an incapacity to see except under a strong light: a case has been recorded, by M. Cunier, of this latter defect having affected eighty-five members of the same family during six generations. The singular incapacity of distinguishing colours, which has been called *Daltonism*, is notoriously hereditary,

and has been traced through five generations, in which it was confined to the female sex.

With respect to the colour of the iris: deficiency of colouring matter is well known to be hereditary in albinoes. The iris of one eye being of a different colour from that of the other, and the iris being spotted, are cases which have been inherited. Mr. Sedgwick gives, in addition, on the authority of Dr. Osborne,[19] the following curious instance of strong inheritance: a family of sixteen sons and five daughters all had eyes "resembling in miniature the markings on the back of a tortoiseshell cat." The mother of this large family had three sisters and a brother all similarly marked, and they derived this peculiarity from their mother, who belonged to a family notorious for transmitting it to their posterity. {10}

Finally, Dr. Lucas emphatically remarks that there is not one single faculty of the eye which is not subject to anomalies; and not one which is not subjected to the principle of inheritance. Mr. Bowman agrees with the general truth of this proposition; which of course does not imply that all malformations are necessarily inherited; this would not even follow if both parents were affected by an anomaly which in most cases was transmissible.

Even if no single fact had been known with respect to the inheritance of disease and malformations by man, the evidence would have been ample in the case of the horse. And this might have been expected, as horses breed much quicker than man, are matched with care, and are highly valued. I have consulted many works, and the unanimity of the belief by veterinaries of all nations in the transmission of various morbid tendencies is surprising. Authors, who have had wide experience, give in detail many singular cases, and assert that contracted feet, with the numerous contingent evils, of ring-bones, curbs, splints, spavin, founder and weakness of the front legs, roaring or broken and thick wind, melanosis, specific ophthalmia, and blindness (the great French veterinary Hazard going so far as to say that a blind race could soon be formed), crib-biting, jibbing, and ill-temper, are all plainly hereditary. Youatt sums up by saying "there is scarcely a malady to which the horse is subject which is not hereditary;" and M. Bernard adds that the doctrine "that there is scarcely a disease which does not run in the stock, is gaining new advocates every day."[20] So it is in regard to cattle, with consumption, good and bad teeth, fine skin, &c. &c. But enough, and more than enough, has been said on disease. Andrew Knight, from his own experience, asserts that disease is hereditary with plants; and this assertion is endorsed by Lindley.[21] {11}

Seeing how hereditary evil qualities are, it is fortunate that good health, vigour, and longevity are equally inherited. It was formerly a well-known practice, when annuities were purchased to be received during the lifetime of a nominee, to search out a person belonging to a family of which many members had lived to extreme old age. As to the inheritance of vigour and endurance, the English race-horse offers an excellent instance. Eclipse begot 334, and King Herod 497 winners. A "cock-tail" is a horse not purely bred, but with only one-eighth or one-sixteenth impure blood in his veins, yet very few instances have ever occurred of such horses having won a great race. They are sometimes as fleet for short distances as thoroughbreds, but as Mr. Robson, the great trainer, asserts, they are deficient in wind, and cannot keep up the pace. Mr. Lawrence also remarks, "perhaps no instance has ever occurred of a three-part-bred horse saving his '*distance*' in running two miles with thoroughbred racers." It has been stated by Cecil, that when unknown horses, whose parents were not celebrated, have unexpectedly won great races, as in the case of Priam, they can always be proved to be descended on both sides, through many generations, from first-rate ancestors. On the Continent, Baron Cameronn challenges, in a German veterinary

periodical, the opponents of the English race-horse, to name one good horse on the Continent which has not some English race-blood in his veins.[22]

With respect to the transmission of the many slight, but infinitely diversified characters, by which the domestic races of animals and plants are distinguished, nothing need be said; for the very existence of persistent races proclaims the power of inheritance. {12}

A few special cases, however, deserve some consideration. It might have been anticipated, that deviations from the law of symmetry would not have been inherited. But Anderson[23] states that a rabbit produced in a litter a young animal having only one ear; and from this animal a breed was formed which steadily produced one-eared rabbits. He also mentions a bitch, with a single leg deficient, and she produced several puppies with the same deficiency. From Hofacker's account[24] it appears that a one-horned stag was seen in 1781 in a forest in Germany, in 1788 two, and afterwards, from year to year, many were observed with only one horn on the right side of the head. A cow lost a horn by suppuration,[25] and she produced three calves which had on the same side of the head, instead of a horn, a small bony lump attached merely to the skin; but we here approach the doubtful subject of inherited mutilations. A man who is left-handed, and a shell in which the spire turns in the wrong direction, are departures from the normal though a symmetrical condition, and they are well known to be inherited.

Polydactylism.—Supernumerary fingers and toes are eminently liable, as various authors have insisted, to transmission, but they are noticed here chiefly on account of their occasional regrowth after amputation. Polydactylism graduates[26] by multifarious steps from a mere cutaneous appendage, not including any bone, to a double hand. But an additional digit, supported on a metacarpal bone, and furnished with all the proper muscles, nerves, and vessels, is sometimes so perfect, that it escapes detection, unless the fingers are actually counted. Occasionally there are several supernumerary digits; but usually only one, making the total number six. This one may represent either a thumb or finger, being attached to the inner or outer margin of the hand. Generally, through the law of correlation, both hands and feet are similarly affected. I have tabulated the cases recorded in various works or privately communicated to me, of forty-six persons with extra digits on one or both hands and feet; if in each case all four extremities had been similarly affected, the table would have shown a total of ninety-two hands and ninety-two feet each with six digits. As it is, seventy-three hands and seventy-five feet were thus affected. This proves, in contradiction to the result arrived at by Dr. Struthers,[27] that the hands are not more frequently affected than the feet. {13}

The presence of more than five digits is a great anomaly, for this number is not normally exceeded by any mammal, bird, or existing reptile.[28] Nevertheless, supernumerary digits are strongly inherited; they have been transmitted through five generations; and in some cases, after disappearing for one, two, or even three generations, have reappeared through reversion. These facts are rendered, as Professor Huxley has observed, more remarkable from its being known in most cases that the affected person had not married one similarly affected. In such cases the child of the fifth generation would have only 1-32nd part of the blood of his first sedigitated ancestor. Other cases are rendered remarkable by the affection gathering force, as Dr. Struthers has shown, in each generation, though in each the affected person had married one not affected; moreover such additional digits are often amputated soon after birth, and can seldom have been strengthened by use. Dr. Struthers gives the following instance: in the first generation an additional digit appeared on one hand; in the second, on both hands; in the third, three brothers had both hands, and one of the brothers a foot affected; and in the fourth generation all four limbs were affected. Yet

we must not over-estimate the force of inheritance. Dr. Struthers asserts that cases of non-inheritance and of the first appearance of additional digits in unaffected families are much more frequent than cases of inheritance. Many other deviations of structure, of a nature almost as anomalous as supernumerary digits, such as deficient phalanges, thickened joints, crooked fingers, &c., are in like manner strongly inherited, and are equally subject to intermission with reversion, though in such cases there is no reason to suppose that both parents had been similarly affected.[29]

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Additional digits have been observed in negroes as well as in other races of man, and in several of the lower animals. Six toes have been described on the hind feet of the newt (*Salamandra cristata*), and, as it is said, of the frog. It deserves notice from what follows, that the six-toed newt, though adult, had preserved some of its larval characters; for part of the hyoidal apparatus, which is properly absorbed during the act of metamorphosis, was retained. In the dog, six toes on the hinder feet have been transmitted through three generations; and I have heard of a race of six-toed cats. In several breeds of the fowl the hinder toe is double, and is generally transmitted truly, as is well shown when Dorkings are crossed with common four-toed breeds.[30] With animals which have properly less than five digits, the number is sometimes increased to five, especially in the front legs, though rarely carried beyond that number; but this is due to the development of a digit already existing in a more or less rudimentary state. Thus the dog has properly four toes behind, but in the larger breeds a fifth toe is commonly, though not perfectly, developed. Horses, which properly have one toe alone fully developed with rudiments of the others, have been described with each foot bearing two or three small separate hoofs: analogous facts have been noticed with sheep, goats, and pigs.[31]

The most interesting point with respect to supernumerary digits is their occasional regrowth after amputation. Mr. White[32] describes a child, three years old, with a thumb double from the first joint. He removed the lesser thumb, which was furnished with a nail; but to his astonishment it grew again, and reproduced a nail. The child was then taken to an eminent London surgeon, and the newly-grown thumb was wholly removed by its socket-joint, but again it grew and reproduced a nail. Dr. Struthers mentions a case of partial regrowth of an additional thumb, amputated when the child was three months old; and the late Dr. Falconer communicated to me an analogous case which had fallen under his own observation. A gentleman, who first called my attention to this subject, has given me the following facts which occurred in his own family. He himself, two brothers, and a sister were born with an extra digit to each extremity. His parents were not affected, and there was no tradition in the family, or in the village in which the family had long resided, of any member having been thus affected. Whilst a child, both additional toes, which were attached by bones, were rudely cut off; but the stump of one grew again, and a second operation was performed in his thirty-third year.

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He has had fourteen children, of whom three have inherited additional digits; and one of them, when about six weeks old, was operated on by an eminent surgeon. The additional finger, which was attached by bone to the outer side of the hand, was removed at the joint; the wound healed, but immediately the digit began growing; and in about three months' time the stump was removed for the second time by the root. But it has since grown again, and is now fully a third of an inch in length, including a bone; so that it will for the third time have to be operated on.

Now the normal digits in adult man and other mammals, in birds, and, as I believe, in true reptiles, have no power of regrowth. The nearest approach to this power is exhibited by the occasional reappearance in man of imperfect nails on the stumps of

his fingers after amputation.[33] But man in his embryonic condition has a considerable power of reproduction, for Sir J. Simpson[34] has several times observed arms which had been cut off in the womb by bands of false membrane, and which had grown again to a certain extent. In one instance, the extremity was "divided into three minute nodules, on two of which small points of nails could be detected;" so that these nodules clearly represented fingers in process of regrowth. When, however, we descend to the lower vertebrate classes, which are generally looked at as representing the higher classes in their embryonic condition, we find ample powers of regrowth. Spallanzani[35] cut off the legs and tail of a salamander six times, and Bonnet eight times, successively, and they were reproduced. An additional digit beyond the proper number was occasionally formed after Bonnet had cut off or had divided longitudinally the hand or foot, and in one instance three additional digits were thus formed.[36] These latter cases appear at first sight quite distinct from the congenital production of additional digits in the higher animals; but theoretically, as we shall see in a future chapter, they probably present no real difference. The larvæ or tadpoles of the tailless Batrachians, but not the adults,[37] are capable of reproducing lost members.[38] Lastly, as I have been informed by Mr. J. J. Briggs and Mr. F. Buckland, when portions of the pectoral and tail fins of various fresh-water fish are cut off, they are perfectly reproduced in about six weeks' time. {16}

From these several facts we may infer that supernumerary digits in man retain to a certain extent an embryonic condition, and that they resemble in this respect the normal digits and limbs in the lower vertebrate classes. They also resemble the digits of some of the lower animals in the number exceeding five; for no mammal, bird, existing reptile, or amphibian (unless the tubercle on the hind feet of the toad and other tailless Batrachians be viewed as a digit) has more than five; whilst fishes sometimes have in their pectoral fins as many as twenty metacarpal and phalangeal bones, which, together with the bony filaments, apparently represent our digits with their nails. So, again, in certain extinct reptiles, namely, the Ichthyopterygia, "the digits may be seven, eight, or nine in number, a significant mark," says Professor Owen, "of piscine affinity."[39]

We encounter much difficulty in attempting to reduce these various facts to any rule or law. The inconstant number of the additional digits—their irregular attachment to either the inner or outer margin of the hand—the gradation which can be traced from a mere loose rudiment of a single digit to a completely double hand—the occasional appearance of additional digits in the salamander after a limb has been amputated—these various facts appear to indicate mere fluctuating monstrosity; and this perhaps is all that can be safely said. Nevertheless, as supernumerary digits in the higher animals, from their power of regrowth and from the number thus acquired exceeding five, partake of the nature of the digits in the lower vertebrate animals;—as they occur by no means rarely, and are transmitted with remarkable strength, though perhaps not more strongly than some other anomalies;—and as with animals which have fewer than five digits, when an additional one appears it is generally due to the development of a visible rudiment;—we are led in all cases to suspect, that, although no actual rudiment can be detected, yet that a latent tendency to the formation of an additional digit exists in all mammals, including man. On this view, as we shall more plainly see in the next chapter when discussing latent tendencies, we should have to look at the whole case as one of reversion to an enormously remote, lowly-organised, and multidigitate progenitor. {17}

I may here allude to a class of facts closely allied to, but somewhat different from, ordinary cases of inheritance. Sir H. Holland[40] states that brothers and sisters of the same family are frequently affected, often at about the same age, by the same peculiar disease, not known to

have previously occurred in the family. He specifies the occurrence of diabetes in three brothers under ten years old; he also remarks that children of the same family often exhibit in common infantile diseases the same peculiar symptoms. My father mentioned to me the case of four brothers who died between the ages of sixty and seventy, in the same highly peculiar comatose state. An instance has been already given of supernumerary digits appearing in four children out of six in a previously unaffected family. Dr. Devay states[41] that two brothers married two sisters, their first-cousins, none of the four nor any relation being an albino; but the seven children produced from this double marriage were all perfect albinoes. Some of these cases, as Mr. Sedgwick[42] has shown, are probably the result of reversion to a remote ancestor, of whom no record had been preserved; and all these cases are so far directly connected with inheritance that no doubt the children inherited a similar constitution from their parents, and, from being exposed to nearly similar conditions of life, it is not surprising that they should be affected in the same manner and at the same period of life.

Most of the facts hitherto given have served to illustrate the force of inheritance, but we must now consider cases, grouped as well as the subject allows into classes, showing how feeble, capricious, or deficient the power of inheritance sometimes is. When a new peculiarity first appears, we can never predict whether it will be inherited. If both parents from their birth present the same peculiarity, the probability is strong that it will be {18} transmitted to at least some of their offspring. We have seen that variegation is transmitted much more feebly by seed from a branch which had become variegated through bud-variation, than from plants which were variegated as seedlings. With most plants the power of transmission notoriously depends on some innate capacity in the individual: thus Vilmorin[43] raised from a peculiarly coloured balsam some seedlings, which all resembled their parent; but of these seedlings some failed to transmit the new character, whilst others transmitted it to all their descendants during several successive generations. So again with a variety of the rose, two plants alone out of six were found by Vilmorin to be capable of transmitting the desired character.

The weeping or pendulous growth of trees is strongly inherited in some cases, and, without any assignable reason, feebly in other cases. I have selected this character as an instance of capricious inheritance, because it is certainly not proper to the parent-species, and because, both sexes being borne on the same tree, both tend to transmit the same character. Even supposing that there may have been in some instances crossing with adjoining trees of the same species, it is not probable that all the seedlings would have been thus affected. At Moccas Court there is a famous weeping oak; many of its branches "are 30 feet long, and no thicker in any part of this length than a common rope:" this tree transmits its weeping character, in a greater or less degree, to all its seedlings; some of the young oaks being so flexible that they have to be supported by props; others not showing the weeping tendency till about twenty years old.[44] Mr. Rivers fertilized, as he informs me, the flowers of a new Belgian weeping thorn (*Cratægus oxyacantha*) with pollen from a crimson not-weeping variety, and three young trees, "now six or seven years old, show a decided tendency to be pendulous, but as yet are not so much so as the mother-plant." According to Mr. MacNab,[45] seedlings from a magnificent weeping birch (*Betula alba*), in the Botanic Garden at Edinburgh, grew for the first ten or fifteen years upright, but then all became weepers like their parent. A peach with pendulous branches, like those of the weeping willow, has been found capable of propagation by seed.[46] Lastly, a weeping and almost prostrate yew (*Taxus baccata*) was found in a hedge in Shropshire; it was a male, but one branch bore female flowers, and produced berries; these, being sown, {19}

produced seventeen trees, all of which had exactly the same peculiar habit with the parent-tree.[47]

These facts, it might have been thought, would have been sufficient to render it probable that a pendulous habit would in all cases be strictly inherited. But let us look to the other side. Mr. MacNab[48] sowed seeds of the weeping beech (*Fagus sylvanica*), but succeeded in raising only common beeches. Mr. Rivers, at my request, raised a number of seedlings from three distinct varieties of weeping elm; and at least one of the parent-trees was so situated that it could not have been crossed by any other elm; but none of the young trees, now about a foot or two in height, show the least signs of weeping. Mr. Rivers formerly sowed above twenty thousand seeds of the weeping ash (*Fraxinus excelsior*), and not a single seedling was in the least degree pendulous: in Germany, M. Borchmeyer raised a thousand seedlings, with the same result. Nevertheless, Mr. Anderson, of the Chelsea Botanic Garden, by sowing seed from a weeping ash, which was found before the year 1780, in Cambridgeshire, raised several pendulous trees.[49] Professor Henslow also informs me that some seedlings from a female weeping ash in the Botanic Garden at Cambridge were at first a little pendulous, but afterwards became quite upright: it is probable that this latter tree, which transmits to a certain extent its pendulous habit, was derived by a bud from the same original Cambridgeshire stock; whilst other weeping ashes may have had a distinct origin. But the crowning case, communicated to me by Mr. Rivers, which shows how capricious is the inheritance of a pendulous habit, is that a variety of another species of ash (*F. lentiscifolia*) which was formerly pendulous, "now about twenty years old has long lost this habit, every shoot being remarkably erect; but seedlings formerly raised from it were perfectly prostrate, the stems not rising more than two inches above the ground." Thus the weeping variety of the common ash, which has been extensively propagated by buds during a long period, did not, with Mr. Rivers, transmit its character to one seedling out of above twenty thousand; whereas the weeping variety of a second species of ash, which could not, whilst grown in the same garden, retain its own weeping character, transmitted to its seedlings the pendulous habit in excess!

Many analogous facts could be given, showing how apparently capricious is the principle of inheritance. All the seedlings from a variety of the Barberry (*B. vulgaris*) with red leaves inherited the same character; only about one-third of the seedlings of the copper Beech (*Fagus sylvatica*) had purple leaves. Not one out of a hundred seedlings of a variety of the *Cerasus padus*, with yellow fruit, bore yellow fruit: one-twelfth of the seedlings of the variety of *Cornus mascula*, with yellow fruit, came true:[50] and lastly, all the trees raised by my father from a yellow-berried holly (*Ilex aquifolium*), found wild, produced yellow berries. Vilmorin[51] observed in a bed of {20}
Saponaria calabrica an extremely dwarf variety, and raised from it a large number of seedlings; some of these partially resembled their parent, and he selected their seed; but the grandchildren were not in the least dwarfed: on the other hand, he observed a stunted and bushy variety of *Tagetes signata* growing in the midst of the common varieties by which it was probably crossed; for most of the seedlings raised from this plant were intermediate in character, only two perfectly resembling their parent; but seed saved from these two plants reproduced the new variety so truly, that hardly any selection has since been necessary.

Flowers transmit their colour truly, or most capriciously. Many annuals come true: thus I purchased German seeds of thirty-four named sub-varieties of one *race* of ten-week stocks (*Matthiola annua*), and raised a hundred and forty plants, all of which, with the exception of a single plant, came true. In saying this, however, it must be understood that I could distinguish only twenty kinds out of the thirty-four named

sub-varieties; nor did the colour of the flower always correspond with the name affixed to the packet; but I say that they came true, because in each of the thirty-six short rows every plant was absolutely alike, with the one single exception. Again, I procured packets of German seed of twenty-five named varieties of common and quilled asters, and raised a hundred and twenty-four plants; of these, all except ten were true in the above limited sense; and I considered even a wrong shade of colour as false.

It is a singular circumstance that white varieties generally transmit their colour much more truly than any other variety. This fact probably stands in close relation with one observed by Verlot,[52] namely, that flowers which are normally white rarely vary into any other colour. I have found that the white varieties of *Delphinium consolida* and of the Stock are the truest. It is, indeed, sufficient to look through a nurseryman's seed-list, to see the large number of white varieties which can be propagated by seed. The several coloured varieties of the sweet-pea (*Lathyrus odoratus*) are very true; but I hear from Mr. Masters, of Canterbury, who has particularly attended to this plant, that the white variety is the truest. The hyacinth, when propagated by seed, is extremely inconstant in colour, but "white hyacinths almost always give by seed white-flowered plants;"[53] and Mr. Masters informs me that the yellow varieties also reproduce their colour, but of different shades. On the other hand, pink and blue varieties, the latter being the natural colour, are not nearly so true: hence, as Mr. Masters has remarked to me, "we see that a garden variety may acquire a more permanent habit than a natural species;" but it should have been added, that this occurs under cultivation, and therefore under changed conditions.

With many flowers, especially perennials, nothing can be more fluctuating than the colour of the seedlings, as is notoriously the case with verbenas, carnations, dahlias, cinerarias, and others.[54] I sowed seed of twelve named varieties of Snapdragon (*Antirrhinum majus*), and utter confusion was the result. In most cases the extremely fluctuating colour of seedling plants is probably in chief part due to crosses between differently-coloured varieties during previous generations. It is almost certain that this is the case with the polyanthus and coloured primrose (*Primula veris* and *vulgaris*), from their reciprocally dimorphic structure;[55] and these are plants which florists speak of as never come true by seed: but if care be taken to prevent crossing, neither species is by any means very inconstant in colour; thus I raised twenty-three plants from a purple primrose, fertilised by Mr. J. Scott with its own pollen, and eighteen came up purple of different shades, and only five reverted to the ordinary yellow colour: again, I raised twenty plants from a bright-red cowslip, similarly treated by Mr. Scott, and every one perfectly resembled its parent in colour, as likewise did, with the exception of a single plant, 73 grandchildren. Even with the most variable flowers, it is probable that each delicate shade of colour might be permanently fixed so as to be transmitted by seed, by cultivation in the same soil, by long-continued selection, and especially by the prevention of crosses. I infer this from certain annual larkspurs (*Delphinium consolida* and *ajacis*), of which common seedlings present a greater diversity of colour than any other plant known to me; yet on procuring seed of five named German varieties of *D. consolida*, only nine plants out of ninety-four were false; and the seedlings of six varieties of *D. ajacis* were true in the same manner and degree as with the stocks above described. A distinguished botanist maintains that the annual species of Delphinium are always self-fertilised; therefore I may mention that thirty-two flowers on a branch of *D. consolida*, enclosed in a net, yielded twenty-seven capsules, with an average of 17.2 seed in each; whilst five flowers, under the same net, which were artificially fertilised, in the same manner as must be effected by bees during their incessant visits, yielded five capsules with an average of 35.2 fine seed; and this shows that the agency of insects is necessary for the full fertility of this

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plant. Analogous facts could be given with respect to the crossing of many other flowers, such as carnations, &c., of which the varieties fluctuate much in colour.

As with flowers, so with our domesticated animals, no character is more variable than colour, and probably in no animal more so than with the horse. Yet with a little care in breeding, it appears that races of any colour might soon be formed. Hofacker gives the result of matching two hundred and sixteen mares of four different colours with like-coloured stallions, without regard to the colour of their ancestors; and of the two hundred and sixteen colts born, eleven alone failed to inherit the colour of their parents: Autenrieth and Ammon assert that, after two generations, colts of a uniform colour are produced with certainty.[56]

In a few rare cases peculiarities fail to be inherited, apparently from the force of inheritance being too strong. I have been assured by breeders of the canary-bird that to get a good jonquil-coloured bird it does not answer to pair two jonquils, as the colour then comes out too strong, or is even brown. So again, if two crested canaries are paired, the young birds rarely inherit this character:[57] for in crested birds a narrow space of bare skin is left on the back of the head, where the feathers are up-turned to form the crest, and, when both parents are thus characterised, the bareness becomes excessive, and the crest itself fails to be developed. Mr. Hewitt, speaking of Laced Sebright Bantams, says[58] that, "why this should be so, I know not, but I am confident that those that are best laced frequently produce offspring very far from perfect in their markings, whilst those exhibited by myself, which have so often proved successful, were bred from the union of heavily-laced birds with those that were scarcely sufficiently laced." {22}

It is a singular fact that, although several deaf-mutes often occur in the same family, and though their cousins and other relations are often in the same condition, yet their parents are very rarely deaf-mutes. To give a single instance: not one scholar out of 148, who were at the same time in the London Institution, was the child of parents similarly afflicted. So again, when a male or a female deaf-mute marries a sound person, their children are most rarely affected: in Ireland out of 203 children thus produced one alone was mute. Even when both parents have been deaf-mutes, as in the case of forty-one marriages in the United States and of six in Ireland, only two deaf and dumb children were produced. Mr. Sedgwick, [59] in commenting on this remarkable and fortunate failure in the power of transmission in the direct line, remarks that it may possibly be owing to "excess having reversed the action of some natural law in development." But it is safer in the present state of our knowledge to look at the whole case as simply unintelligible.

With respect to the inheritance of structures mutilated by injuries or altered by disease it is difficult to come to any definite conclusion. In some cases mutilations have been practised for a vast number of generations without any inherited result. Godron has remarked[60] that different races of man have from time immemorial knocked out their upper incisors, cut off joints of their fingers, made holes of immense size through the lobes of their ears or through their nostrils, made deep gashes in various parts of their bodies, and there is no reason whatever to suppose that these mutilations have ever been inherited. Adhesions due to inflammation and pits from the small-pox (and formerly many consecutive generations must have been thus pitted) are not inherited. With respect to Jews, I have been assured by three medical men of the Jewish faith that circumcision, which has been practised for so many ages, has produced no inherited effect; Blumenbach, on the other hand, asserts[61] that in Germany Jews are often born in a condition rendering circumcision difficult, so that a name is here applied to them signifying "born circumcised." The oak and other trees must have borne galls from primeval times, yet they do not produce inherited excrescences; many other such facts could be adduced. {23}

On the other hand, various cases have been recorded of cats, dogs, and horses, which have had their tails, legs, &c., amputated or injured, producing offspring with the same parts ill-formed; but as it is not at all rare for similar malformations to appear spontaneously, all such cases may be due to mere coincidence. Nevertheless, Dr. Prosper Lucas has given, on good authorities, such a long list of inherited injuries, that it is difficult not to believe in them. Thus, a cow that had lost a horn from an accident with consequent suppuration, produced three calves which were hornless on the same side of the head. With the horse, there seems hardly a doubt that bony exostoses on the legs, caused by too much travelling on hard roads, are inherited. Blumenbach records the case of a man who had his little finger on the right hand almost cut off, and which in consequence grew crooked, and his sons had the same finger on the same hand similarly crooked. A soldier, fifteen years before his marriage, lost his left eye from purulent ophthalmia, and his two sons were microphthalmic {24} on the same side.[62] In all such cases, if truthfully reported, in which the parent has had an organ injured on one side, and more than one child has been born with the same organ affected on the same side, the chances against mere coincidence are enormous. But perhaps the most remarkable and trustworthy fact is that given by Dr. Brown-Séquard,[63] namely, that many young guinea-pigs inherited an epileptic tendency from parents which had been subjected to a particular operation, inducing in the course of a few weeks a convulsive disease like epilepsy: and it should be especially noted that this eminent physiologist bred a large number of guinea-pigs from animals which had not been operated on, and not one of these manifested the epileptic tendency. On the whole, we can hardly avoid admitting, that injuries and mutilations, especially when followed by disease, or perhaps exclusively when thus followed, are occasionally inherited.

Although many congenital monstrosities are inherited, of which examples have already been given, and to which may be added the lately recorded case of the transmission during a century of hare-lip with a cleft-palate in the writer's own family,[64] yet other malformations are rarely or never inherited. Of these later cases, many are probably due to injuries in the womb or egg, and would come under the head of non-inherited injuries or mutilations. With plants, a long catalogue of inherited monstrosities of the most serious and diversified nature could easily be given; and with plants, there is no reason to suppose that monstrosities are caused by direct injuries to the seed or embryo.

Causes of Non-inheritance.

A large number of cases of non-inheritance are intelligible on the principle, that a strong tendency to inheritance does exist, but that it is overborne by hostile or unfavourable {25} conditions of life. No one would expect that our improved pigs, if forced during several generations to travel about and root in the ground for their own subsistence, would transmit, as truly as they now do, their tendency to fatten, and their short muzzles and legs. Dray-horses assuredly would not long transmit their great size and massive limbs, if compelled to live on a cold, damp mountainous region; we have indeed evidence of such deterioration in the horses which have run wild on the Falkland Islands. European dogs in India often fail to transmit their true character. Our sheep in tropical countries lose their wool in a few generations. There seems also to be a close relation between certain peculiar pastures and the inheritance of an enlarged tail in fat-tailed sheep, which form one of the most ancient breeds in the world. With plants, we have seen that the American varieties of maize lose their proper character in the course of two or three generations, when cultivated in Europe. Our cabbages, which here come so true by seed, cannot form heads in hot countries. Under changed circumstances, periodical habits of life soon fail to be transmitted, as the period of maturity in summer and winter wheat, barley, and vetches. So it is with animals; for instance, a person whose statement I can trust, procured eggs of Aylesbury ducks from that town, where they are kept in houses and are reared as early as possible for the London market; the ducks bred from these eggs in a distant part of England, hatched their first brood

on January 24th, whilst common ducks, kept in the same yard and treated in the same manner, did not hatch till the end of March; and this shows that the period of hatching was inherited. But the grandchildren of these Aylesbury ducks completely lost their early habit of incubation, and hatched their eggs at the same time with the common ducks of the same place.

Many cases of non-inheritance apparently result from the conditions of life continually inducing fresh variability. We have seen that when the seeds of pears, plums, apples, &c., are sown, the seedlings generally inherit some degree of family likeness from the parent-variety. Mingled with these seedlings, a few, and sometimes many, worthless, wild-looking plants commonly appear; and their appearance may be attributed to the principle of reversion. But scarcely a single seedling will be found perfectly to resemble the parent- {26}
form; and this, I believe, may be accounted for by constantly recurring variability induced by the conditions of life. I believe in this, because it has been observed that certain fruit-trees truly propagate their kind whilst growing on their own roots, but when grafted on other stocks, and by this process their natural state is manifestly affected, they produce seedlings which vary greatly, departing from the parental type in many characters.[65] Metzger, as stated in the ninth chapter, found that certain kinds of wheat brought from Spain and cultivated in Germany, failed during many years to reproduce themselves truly; but that at last, when accustomed to their new conditions, they ceased to be variable,—that is, they became amenable to the power of inheritance. Nearly all the plants which cannot be propagated with any approach to certainty by seed, are kinds which have long been propagated by buds, cuttings, offsets, tubers, &c., and have in consequence been frequently exposed during their individual lives to widely diversified conditions of life. Plants thus propagated become so variable, that they are subject, as we have seen in the last chapter, even to bud-variation. Our domesticated animals, on the other hand, are not exposed during their individual lives to such extremely diversified conditions, and are not liable to such extreme variability; therefore they do not lose the power of transmitting most of their characteristic features. In the foregoing remarks on non-inheritance, crossed breeds are of course excluded, as their diversity mainly depends on the unequal development of characters derived from either parent, modified by the principles of reversion and prepotency.

Conclusion.

It has, I think, been shown in the early part of this chapter how strongly new characters of the most diversified nature, whether normal or abnormal, injurious or beneficial, whether affecting organs of the highest or most trifling importance, are inherited. Contrary to the common opinion, it is often sufficient for the inheritance of some peculiar character, that one parent alone should possess it, as in most cases in which the rarer anomalies have been {27}
transmitted. But the power of transmission is extremely variable: in a number of individuals descended from the same parents, and treated in the same manner, some display this power in a perfect manner, and in some it is quite deficient; and for this difference no reason can be assigned. In some cases the effects of injuries or mutilations apparently are inherited; and we shall see in a future chapter that the effects of the long-continued use and disuse of parts are certainly inherited. Even those characters which are considered the most fluctuating, such as colour, are with rare exceptions transmitted much more forcibly than is generally supposed. The wonder, indeed, in all cases is not that any character should be transmitted, but that the power of inheritance should ever fail. The checks to inheritance, as far as we know them, are, firstly, circumstances hostile to the particular character in question; secondly, conditions of life incessantly inducing fresh variability; and lastly, the crossing of distinct varieties during some previous generation, together with reversion or atavism—that is, the tendency in the child to resemble its grand-parents or more remote ancestors instead of its immediate parents. This latter subject will be fully discussed in the following chapter.

CHAPTER XIII. {28}

INHERITANCE *continued*—REVERSION OR ATAVISM.

DIFFERENT FORMS OF REVERSION—IN PURE OR UNCROSSED BREEDS, AS IN PIGEONS, FOWLS, HORNLESS CATTLE AND SHEEP, IN CULTIVATED PLANTS—REVERSION IN FERAL ANIMALS AND PLANTS—REVERSION IN CROSSED VARIETIES AND SPECIES—REVERSION THROUGH BUD-PROPAGATION, AND BY SEGMENTS IN THE SAME FLOWER OR FRUIT—IN DIFFERENT PARTS OF THE BODY IN THE SAME ANIMAL—THE ACT OF CROSSING A DIRECT CAUSE OF REVERSION, VARIOUS CASES OF, WITH INSTINCTS—OTHER PROXIMATE CAUSES OF REVERSION—LATENT CHARACTERS—SECONDARY SEXUAL CHARACTERS—UNEQUAL DEVELOPMENT OF THE TWO SIDES OF THE BODY—APPEARANCE WITH ADVANCING AGE OF CHARACTERS DERIVED FROM A CROSS—THE GERM WITH ALL ITS LATENT CHARACTERS A WONDERFUL OBJECT—MONSTROSITIES—PELORIC FLOWERS DUE IN SOME CASES TO REVERSION.

The great principle of inheritance to be discussed in this chapter has been recognised by agriculturists and authors of various nations, as shown by the scientific term *Atavism*, derived from atavus, an ancestor; by the English terms of *Reversion*, or *Throwing back*; by the French *Pas-en-arrière*; and by the German *Rück-schlag*, or *Rück-schritt*. When the child resembles either grandparent more closely than its immediate parents, our attention is not much arrested, though in truth the fact is highly remarkable; but when the child resembles some remote ancestor, or some distant member in a collateral line,—and we must attribute the latter case to the descent of all the members from a common progenitor,—we feel a just degree of astonishment. When one parent alone displays some newly-acquired and generally inheritable character, and the offspring do not inherit it, the cause may lie in the other parent having the power of prepotent transmission. But when both parents are similarly characterised, and the child does not, whatever the cause may be, inherit the character in question, but resembles its grandparents, we have one of the simplest cases of reversion. We continually see another and even more simple case of atavism, though not generally included under this head, namely, when the son more closely resembles his {29} maternal than his paternal grandsire in some male attribute, as in any peculiarity in the beard of man, the horns of the bull, the hackles or comb of the cock, or, as in certain diseases necessarily confined to the male sex; for the mother cannot possess or exhibit such male attributes, yet the child has inherited them, through her blood, from his maternal grandsire.

The cases of reversion may be divided into two main classes, which, however, in some instances, blend into each other; namely, first, those occurring in a variety or race which has not been crossed, but has lost by variation some character that it formerly possessed, and which afterwards reappears. The second class includes all cases in which a distinguishable individual, sub-variety, race, or species, has at some former period been crossed with a distinct form, and a character derived from this cross, after having disappeared during one or several generations, suddenly reappears. A third class, differing only in the manner of reproduction, might be formed to include all cases of reversion effected by means of buds, and therefore independent of true or seminal generation. Perhaps even a fourth class might be instituted, to include reversions by segments in the same individual flower or fruit, and in different parts of the body in the same individual animal as it grows old. But the two first main classes will be sufficient for our purpose.

Reversion to lost Characters by pure or uncrossed forms.—Striking instances of this first class of cases were given in the sixth chapter, namely, of the occasional reappearance, in variously-coloured pure breeds of the pigeon, of blue birds with all the marks which characterise the wild *Columba livia*. Similar cases were given in the case of the fowl. With

the common ass, as we now know that the legs of the wild progenitor are striped, we may feel assured that the occasional appearance of such stripes in the domestic animal is a case of simple reversion. But I shall be compelled to refer again to these cases, and therefore will here pass them over.

The aboriginal species from which our domesticated cattle and sheep are descended, no doubt possessed horns; but several hornless breeds are now well established. Yet in these—for instance, in Southdown sheep—"it is not unusual to find among the male lambs some {30} with small horns." The horns, which thus occasionally reappear in other polled breeds, either "grow to the full size, or are curiously attached to the skin alone and hang loosely down, or drop off."[66] The Galloways and Suffolk cattle have been hornless for the last 100 or 150 years, but a horned calf, with the horn often loosely attached, is occasionally born. [67]

There is reason to believe that sheep in their early domesticated condition were "brown or dingy black;" but even in the time of David certain flocks were spoken of as white as snow. During the classical period the sheep of Spain are described by several ancient authors as being black, red, or tawny.[68] At the present day, notwithstanding the great care which is taken to prevent it, particoloured lambs and some entirely black are occasionally dropped by our most highly improved and valued breeds, such as the Southdowns. Since the time of the famous Bakewell, during the last century, the Leicester sheep have been bred with the most scrupulous care; yet occasionally grey-faced, or black-spotted, or wholly black lambs appear.[69] This occurs still more frequently with the less improved breeds, such as the Norfolks.[70] As bearing on this tendency in sheep to revert to dark colours, I may state (though in doing so I trench on the reversion of crossed breeds, and likewise on the subject of prepotency) that the Rev. W. D. Fox was informed that seven white Southdown ewes were put to a so-called Spanish ram, which had two small black spots on his sides, and they produced thirteen lambs, all perfectly black. Mr. Fox believes that this ram belonged to a breed which he has himself kept, and which is always spotted with black and white; and he finds that Leicester sheep crossed by rams of this breed always produce black lambs: he has gone on recrossing these crossed sheep with pure white Leicesters during three successive generations, but always with the same result. Mr. Fox was also told by the friend from {31} whom the spotted breed was procured, that he likewise had gone on for six or seven generations crossing with white sheep, but still black lambs were invariably produced.

Similar facts could be given with respect to tailless breeds of various animals. For instance, Mr. Hewitt[71] states that chickens bred from some Rumpless fowls, which were reckoned so good that they won a prize at an exhibition, "in a considerable number of instances were furnished with fully developed tail-feathers." On inquiry, the original breeder of these fowls stated that, from the time when he had first kept them, they had often produced fowls furnished with tails; but that these latter would again reproduce rumpless chickens.

Analogous cases of reversion occur in the vegetable kingdom; thus "from seeds gathered from the finest cultivated varieties of Heartsease (*Viola tricolor*), plants perfectly wild both in their foliage and their flowers are frequently produced;"[72] but the reversion in this instance is not to a very ancient period, for the best existing varieties of the heartsease are of comparatively modern origin. With most of our cultivated vegetables there is some tendency to reversion to what is known to be, or may be presumed to be, their aboriginal state; and this would be more evident if gardeners did not generally look over their beds of seedlings, and pull up the false plants or "rogues" as they are called. It has already been remarked, that some few seedling apples and pears generally resemble, but apparently are not identical with, the wild trees from which they are descended. In our turnip[73] and carrot-beds a few plants often "break"—that is, flower too soon; and their roots are generally found to be hard and stringy, as in the parent-species. By the aid of a little

selection, carried on during a few generations, most of our cultivated plants could probably be brought back, without any great change in their conditions of life, to a wild or nearly wild condition: Mr. Buckman has effected this with the parsnip;[74] and Mr. Hewett C. Watson, as he informs me, selected, during three generations, "the most diverging plants of Scotch kail, perhaps one of the least modified varieties of the cabbage; and in the third generation some of the plants came very close to the forms now established in England about old castle-walls, and called indigenous." {32}

Reversion in Animals and Plants which have run wild.—In the cases hitherto considered, the reverting animals and plants have not been exposed to any great or abrupt change in their conditions of life which could have induced this tendency; but it is very different with animals and plants which have become feral or run wild. It has been repeatedly asserted in the most positive manner by various authors, that feral animals and plants invariably return to their primitive specific type. It is curious on what little evidence this belief rests. Many of our domesticated animals could not subsist in a wild state; thus, the more highly improved breeds of the pigeon will not "field" or search for their own food. Sheep have never become feral, and would be destroyed by almost every beast of prey. In several cases we do not know the aboriginal parent-species, and cannot possibly tell whether or not there has been any close degree of reversion. It is not known in any instance what variety was first turned out; several varieties have probably in some cases run wild, and their crossing alone would tend to obliterate their proper character. Our domesticated animals and plants, when they run wild, must always be exposed to new conditions of life, for, as Mr. Wallace[75] has well remarked, they have to obtain their own food, and are exposed to competition with the native productions. Under these circumstances, if our domesticated animals did not undergo change of some kind, the result would be quite opposed to the conclusions arrived at in this work. Nevertheless, I do not doubt that the simple fact of animals and plants becoming feral, does cause some tendency to reversion to the primitive state; though this tendency has been much exaggerated by some authors.

I will briefly run through the recorded cases. With neither horses nor cattle is the primitive stock known; and it has been shown in former chapters that they have assumed different colours in different countries. Thus the horses which have run wild in South America are generally brownish-bay, and in the East dun-coloured; their heads have become larger and coarser, and this may be due to reversion. No careful description has been given of the feral goat. Dogs which have run wild in various countries have hardly anywhere assumed a uniform character; but they are probably descended from several domestic races, and aboriginally from several distinct species. Feral cats, both in Europe and La Plata, are regularly striped; in some cases they have grown to an unusually large size, but do not differ from the domestic animal in any other character. When variously-coloured tame rabbits are turned out in Europe, they generally reacquire the colouring of the wild animal; there can be no doubt that this does really occur, but we should remember that oddly-coloured and conspicuous animals would suffer much from beasts of prey and from being easily shot; this at least was the opinion of a gentleman who tried to stock his woods with a nearly white variety; and when thus destroyed, they would in truth be supplanted by, instead of being transformed into, the common rabbit. We have seen that the feral rabbits of Jamaica, and especially of Porto Santo, have assumed new colours and other new characters. The best known case of reversion, and that on which the widely-spread belief in its universality apparently rests, is that of pigs. These animals have run wild in the West Indies, South America, and the Falkland Islands, and have everywhere acquired the dark colour, the thick bristles, and great tusks of the wild boar; and the young have reacquired longitudinal stripes. But even in the case of the pig, Roulin describes the half-wild animals in different parts of South America as differing in {33}

several respects. In Louisiana the pig[76] has run wild, and is said to differ a little in form, and much in colour, from the domestic animal, yet does not closely resemble the wild boar of Europe. With pigeons and fowls,[77] it is not known what variety was first turned out, nor what character the feral birds have assumed. The guinea-fowl in the West Indies, when feral, seems to vary more than in the domesticated state.

With respect to plants run wild, Dr. Hooker[78] has strongly insisted on what slight evidence the common belief in their power of reversion rests. Godron[79] describes wild turnips, carrots, and celery; but these plants in their cultivated state hardly differ from their wild prototypes, except in the succulency and enlargement of certain parts, {34}
—characters which would be surely lost by plants growing in a poor soil and struggling with other plants. No cultivated plant has run wild on so enormous a scale as the cardoon (*Cynara cardunculus*) in La Plata. Every botanist who has seen it growing there, in vast beds, as high as a horse's back, has been struck with its peculiar appearance; but whether it differs in any important point from the cultivated Spanish form, which is said not to be prickly like its American descendant, or whether it differs from he wild Mediterranean species, which is said not to be social, I do not know.

Reversion to Characters derived from a Cross, in the case of Sub-varieties, Races, and Species.—When an individual having some recognizable peculiarity unites with another of the same sub-variety, not having the peculiarity in question, it often reappears in the descendants after an interval of several generations. Every one must have noticed, or heard from old people of children closely resembling in appearance or mental disposition, or in so small and complex a character as expression, one of their grandparents, or some more distant collateral relation. Very many anomalies of structure and diseases,[80] of which instances have been given in the last chapter, have come into a family from one parent, and have reappeared in the progeny after passing over two or three generations. The following case has been communicated to me on good authority, and may, I believe, be fully trusted: a pointer-bitch produced seven puppies; four were marked with blue and white, which is so unusual a colour with pointers that she was thought to have played false with one of the greyhounds, and the whole litter was condemned; but the gamekeeper was permitted to save one as a curiosity. Two years afterwards a friend of the owner saw the young dog, and declared that he was the image of his old pointer-bitch Sappho, the only blue and white pointer of pure descent which he had ever seen. This led to close inquiry, and it was proved that he was the great-great-grandson of Sappho; so that, according to the common expression, he had only 1-16th of her blood in his veins. Here it can hardly be doubted that a character derived from a cross with an individual of the same variety reappeared after passing over three generations.

When two distinct races are crossed, it is notorious that the tendency in the offspring to {35}
revert to one or both parent-forms is strong, and endures for many generations. I have myself seen the clearest evidence of this in crossed pigeons and with various plants. Mr. Sidney[81] states that, in a litter of Essex pigs, two young ones appeared which were the image of the Berkshire boar that had been used twenty-eight years before in giving size and constitution to the breed. I observed in the farmyard at Betley Hall some fowls showing a strong likeness to the Malay breed, and was told by Mr. Tollet that he had forty years before crossed his birds with Malays; and that, though he had at first attempted to get rid of this strain, he had subsequently given up the attempt in despair, as the Malay character would reappear.

This strong tendency in crossed breeds to revert has given rise to endless discussions in how many generations after a single cross, either with a distinct breed or merely with an inferior

animal, the breed may be considered as pure, and free from all danger of reversion. No one supposes that less than three generations suffices, and most breeders think that six, seven, or eight are necessary, and some go to still greater lengths.[82] But neither in the case of a breed which has been contaminated by a single cross, nor when, in the attempt to form an intermediate breed, half-bred animals have been matched together during many generations, can any rule be laid down how soon the tendency to reversion will be obliterated. It depends on the difference in the strength or prepotency of transmission in the two parent-forms, on their actual amount of difference, and on the nature of the conditions of life to which the crossed offspring are exposed. But we must be careful not to confound these cases of reversion to characters gained from a cross, with those given under the first class, in which characters originally common to *both* parents, but lost at some former period, reappear; for such characters may recur after an almost indefinite number of generations.

The law of reversion is equally powerful with hybrids, when they are sufficiently fertile to breed together, or when they are repeatedly crossed with either pure parent-form, as with mongrels. It is not necessary to give instances, for in the case of plants almost every one who has worked on this subject from the time of Kölreuter to the present day has insisted on this tendency. Gärtner has recorded some good instances; but no one has given more striking cases than Naudin.[83] The tendency differs in degree or strength in different groups, and partly depends, as we shall presently see, on the fact of the parent-plants having been long cultivated. Although the tendency to reversion is extremely general with nearly all mongrels and hybrids, it cannot be considered as invariably characteristic of them; there is, also, reason to believe that it may be mastered by long-continued selection; but these subjects will more properly be discussed in a future chapter on Crossing. From what we see of the power and scope of reversion, both in pure races and when varieties or species are crossed, we may infer that characters of almost every kind are capable of reappearance after having been lost for a great length of time. But it does not follow from this that in each particular case certain characters will reappear: for instance, this will not occur when a race is crossed with another endowed with prepotency of transmission. In some few cases the power of reversion wholly fails, without our being able to assign any cause for the failure: thus it has been stated that in a French family in which 85 out of above 600 members, during six generations, had been subject to night-blindness, "there has not been a single example of this affection in the children of parents who were themselves free from it."[84] {36}

Reversion through Bud-propagation—Partial Reversion, by segments in the same flower or fruit, or in different parts of the body in the same individual animal.—In the eleventh chapter, many cases of reversion by buds, independently of seminal generation, were given —as when a leaf-bud on a variegated, curled, or laciniated variety suddenly reassumes its proper character; or as when a Provence-rose appears on a moss-rose, or a peach on a nectarine-tree. In some of these cases only half the flower or fruit, or a smaller segment, or mere stripes, reassumed their former character; and here we have with buds reversion by segments. Vilmorin[85] has also recorded several cases with plants derived from seed, of flowers reverting by stripes or blotches to their primitive colours: he states that in all such cases a white or pale-coloured variety must first be formed, and, when this is propagated for a length of time by seed, striped seedlings occasionally make their appearance; and these can afterwards by care be multiplied by seed. {37}

The stripes and segments just referred to are not due, as far as is known, to reversion to characters derived from a cross, but to characters lost by variation. These cases, however, as Naudin[86] insists in his discussion on disjunction of character, are closely analogous with those given in the eleventh chapter, in which crossed plants are known to have produced half-and-half or striped flowers and fruit, or distinct kinds of flowers on the same root resembling the two parent-forms. Many piebald animals probably come under this same

head. Such cases, as we shall see in the chapter on Crossing, apparently result from certain characters not readily blending together, and, as a consequence of this incapacity for fusion, the offspring either perfectly resemble one of their two parents, or resemble one parent in one part and the other parent in another part; or whilst young are intermediate in character, but with advancing age revert wholly or by segments to either parent-form, or to both. Thus young trees of the *Cytisus adami* are intermediate in foliage and flowers between the two parent-forms; but when older the buds continually revert either partially or wholly to both forms. The cases given in the eleventh chapter on the changes which occurred during growth in crossed plants of Tropæolum, Cereus, Datura, and Lathyrus are all analogous. As {38} however these plants are hybrids of the first generation, and as their buds after a time come to resemble their parents and not their grandparents, these cases do not at first appear to come under the law of reversion in the ordinary sense of the word; nevertheless, as the change is effected through a succession of bud-generations on the same plant, they may be thus included.

Analogous facts have been observed in the animal kingdom, and are more remarkable, as they occur strictly in the same individual, and not as with plants through a succession of bud-generations. With animals the act of reversion, if it can be so designated, does not pass over a true generation, but merely over the early stages of growth in the same individual. For instance, I crossed several white hens with a black cock, and many of the chickens were during the first year perfectly white, but acquired during the second year black feathers; on the other hand, some of the chickens which were at first black became during the second year piebald with white. A great breeder[87] says, that a Pencilled Brahma hen which has any of the blood of the Light Brahma in her, will "occasionally produce a pullet well pencilled during the first year, but she will most likely moult brown on the shoulders and become quite unlike her original colours in the second year." The same thing occurs with Light Brahmas if of impure blood. I have observed exactly similar cases with the crossed offspring from differently coloured pigeons. But here is a more remarkable fact: I crossed a turbit, which has a frill formed by the feathers being reversed on its breast, with a trumpeter; and one of the young pigeons thus raised showed at first not a trace of the frill, but, after moulting thrice, a small yet unmistakably distinct frill appeared on its breast. According to Girou,[88] calves produced from a red cow by a black bull, or from a black cow by a red bull, are not rarely born red, and subsequently become black.

In the foregoing cases, the characters which appear with advancing age are the result of a cross in the previous or some former generation; but in the following cases, the characters {39} which thus reappear formerly appertained to the species, and were lost at a more or less remote epoch. Thus, according to Azara,[89] the calves of a hornless race of cattle which originated in Corrientes, though at first quite hornless, as they become adult sometimes acquire small, crooked, and loose horns; and these in succeeding years occasionally become attached to the skull. White and black bantams, both of which generally breed true, sometimes assume as they grow old a saffron or red plumage. For instance, a first-rate black bantam has been described, which during three seasons was perfectly black, but then annually became more and more red; and it deserves notice that this tendency to change, whenever it occurs in a bantam, "is almost certain to prove hereditary."[90] The cuckoo or blue-mottled Dorking cock, when old, is liable to acquire yellow or orange hackles in place of his proper bluish-grey hackles.[91] Now, as *Gallus bankiva* is coloured red and orange, and as Dorking fowls and both kinds of bantams are descended from this species, we can hardly doubt that the change which occasionally occurs in the plumage of these birds as their age advances, results from a tendency in the individual to revert to the primitive type.

Crossing as a direct cause of Reversion.—It has long been notorious that hybrids and mongrels often revert to both or to one of their parent-forms, after an interval of from two to

seven or eight, or according to some authorities even a greater number of generations. But that the act of crossing in itself gives an impulse towards reversion, as shown by the reappearance of long-lost characters, has never, I believe, been hitherto proved. The proof lies in certain peculiarities, which do not characterise the immediate parents, and therefore cannot have been derived from them, frequently appearing in the offspring of two breeds when crossed, which peculiarities never appear, or appear with extreme rarity, in these same breeds, as long as they are precluded from crossing. As this conclusion seems to me highly {40} curious and novel, I will give the evidence in detail.

My attention was first called to this subject, and I was led to make numerous experiments, by MM. Boitard and Corbié having stated that, when they crossed certain breeds, pigeons coloured like the wild *C. livia*, or the common dovecot, namely, slaty-blue, with double black wing-bars, sometimes chequered with black, white loins, the tail barred with black, with the outer feathers edged with white, were almost invariably produced. The breeds which I crossed, and the remarkable results attained, have been fully described in the sixth chapter. I selected pigeons, belonging to true and ancient breeds, which had not a trace of blue or any of the above specified marks; but when crossed, and their mongrels recrossed, young birds were continually produced, more or less plainly coloured slaty-blue, with some or all of the proper characteristic marks. I may recall to the reader's memory one case, namely, that of a pigeon, hardly distinguishable from the wild Shetland species, the grandchild of a red-spot, white fantail, and two black barbs, from any of which, when purely-bred, the production of a pigeon coloured like the wild *C. livia* would have been almost a prodigy.

I was thus led to make the experiments, recorded in the seventh chapter, on fowls. I selected long-established, pure breeds, in which there was not a trace of red, yet in several of the mongrels feathers of this colour appeared; and one magnificent bird, the offspring of a black Spanish cock and white Silk hen, was coloured almost exactly like the wild *Gallus bankiva*. All who know anything of the breeding of poultry will admit that tens of thousands of pure Spanish and of pure white Silk fowls might have been reared without the appearance of a red feather. The fact, given on the authority of Mr. Tegetmeier, of the frequent appearance, in mongrel fowls, of pencilled or transversely-barred feathers, like those common to many gallinaceous birds, is likewise apparently a case of reversion to a character formerly possessed by some ancient progenitor of the family. I owe to the kindness of this same excellent observer the inspection of some neck-hackles and tail-feathers from a hybrid between the common fowl and a very distinct species, the *Gallus varius*; and these feathers are transversely striped in a conspicuous manner with dark metallic blue and grey, a character which could not have been derived from either immediate parent.

I have been informed by Mr. B. P. Brent, that he crossed a white Aylesbury drake and a black so-called Labrador duck, both of which are true breeds, and he obtained a young drake closely like the mallard (*A. boschas*). Of the musk-duck (*A. moschata*, Linn.) there are two sub-breeds, namely, white and slate-coloured; and these I am informed breed true, or nearly true. But the Rev. W. D. Fox tells me that, by putting a white drake to a slate-coloured duck, black birds, pied with white, like the wild musk-duck, were always produced.

We have seen in the fourth chapter, that the so-called Himalayan rabbit, with its snow-white body, black ears, nose, tail, and feet, breeds perfectly true. This race is known to {41} have been formed by the union of two varieties of silver-grey rabbits. Now, when a Himalayan doe was crossed by a sandy-coloured buck, a silver-grey rabbit was produced; and this is evidently a case of reversion to one of the parent varieties. The young of the Himalayan rabbit are born snow-white, and the dark marks do not appear

until some time subsequently; but occasionally young Himalayan rabbits are born of a light silver-grey, which colour soon disappears; so that here we have a trace of reversion, during an early period of life, to the parent-varieties, independently of any recent cross.

In the third chapter is was shown that at an ancient period some breeds of cattle in the wilder parts of Britain were white with dark ears, and that the cattle now kept half wild in certain parks, and those which have run quite wild in two distant parts of the world, are likewise thus coloured. Now, an experienced breeder, Mr. J. Beasley, of Northamptonshire,[92] crossed some carefully selected West Highland cows with purely-bred shorthorn bulls. The bulls were red, red and white, or dark roan; and the Highland cows were all of a red colour, inclining to a light or yellow shade. But a considerable number of the offspring—and Mr. Beasley calls attention to this as a remarkable fact—were white, or white with red ears. Bearing in mind that none of the parents were white, and that they were purely-bred animals, it is highly probable that here the offspring reverted, in consequence of the cross, to the colour either of the aboriginal parent-species or of some ancient and half-wild parent-breed. The following case, perhaps, comes under the same head: cows in their natural state have their udders but little developed, and do not yield nearly so much milk as our domesticated animals. Now there is some reason to believe[93] that cross-bred animals between two kinds, both of which are good milkers, such as Alderneys and Shorthorns, often turn out worthless in this respect.

In the chapter on the Horse reasons were assigned for believing that the primitive stock was striped and dun-coloured; and details were given, showing that in all parts of the world stripes of a dark colour 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 colours. But the stripes appear most frequently on the various kinds of duns. They may sometimes plainly be seen on foals, and subsequently disappear. The dun-colour and the stripes are strongly transmitted when a horse thus characterised 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, though 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,[94] which is thus striped. In the domestic animal the stripes on the shoulder are occasionally double, or forked at the extremity, as in certain zebrine species. There is reason to believe that the foal is {42}
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-coloured 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-coloured, 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,[95] and remarks, that mules are particularly liable to be thus striped on their legs. In South America, according to Roulin,[96] such stripes are more frequent and conspicuous in the mule than in the ass. In the United States, Mr. Gosse,[97] 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."

Many years ago I saw in the Zoological Gardens a curious triple hybrid, from a bay mare, by a hybrid from a male ass and female zebra. This animal when old had hardly any stripes; but I was assured by the superintendent, that when young it had shoulder-stripes, and faint stripes on its flanks and legs. I mention this case more especially as an instance of the stripes being much plainer during youth than in old age.

As the zebra has such conspicuously striped legs, it might have been expected that the hybrids from this animal and the common ass would have had their legs in some degree striped; but it appears from the figures given in Dr. Gray's 'Knowsley Gleanings,' and still more plainly from that given by Geoffroy and F. Cuvier,[98] that the legs are much more conspicuously striped than the rest of the body; and this fact is intelligible only on the belief that the ass aids in giving, through the power of reversion, this character to its hybrid offspring.

The quagga is banded over the whole front part of its body like a zebra, but has no stripes on its legs, or mere traces of them. But in the famous hybrid bred by Lord Morton,[99] from a chesnut, nearly purely-bred, Arabian mare, by a male quagga, the stripes were "more strongly defined and darker than those on the legs of the quagga." The mare was subsequently put to a black Arabian horse, and bore two colts, both of which, as formerly stated, were plainly striped on the legs, and one of them likewise had stripes on the neck and body.

The *Asinus Indicus*[100] is characterised by a spinal stripe, without shoulder or leg stripes; but traces of these latter stripes may occasionally be seen even in the adult; [101] and Colonel S. Poole, who has had ample opportunities for observation, informs me that in the foal, when first born, the head and legs are often striped, but the shoulder-stripe is not so distinct as in the domestic ass; all these stripes, excepting that along the spine, soon disappear. Now a hybrid, raised at Knowsley[102] from a female of this species by a male domestic ass, had all four legs transversely and conspicuously striped, had three short stripes on each shoulder, and had even some zebra-like stripes on its face! Dr. Gray informs me that he has seen a second hybrid of the same parentage similarly striped. {43}

From these facts we see that the crossing of the several equine species tends in a marked manner to cause stripes to appear on various parts of the body, especially on the legs. As we do not know whether the primordial parent of the genus was striped, the appearance of the stripes can only hypothetically be attributed to reversion. But most persons, after considering the many undoubted cases of variously coloured marks reappearing by reversion in crossed pigeons, fowls, ducks, &c., will come to the same conclusion with respect to the horse-genus; and in this case we must admit that the progenitor of the group was striped on the legs, shoulders, face, and probably over the whole body, like a zebra. If we reject this view, the frequent and almost regular appearance of stripes in the several foregoing hybrids is left without any explanation.

It would appear that with crossed animals a similar tendency to the recovery of lost characters holds good even with instincts. There are some breeds of fowls which are called "everlasting layers," because they have lost the instinct of incubation; and so rare is it for them to incubate that I have seen notices published in works on poultry, when hens of such breeds have taken to sit.[103] Yet the aboriginal species was of course a good incubator; for with birds in a state of nature hardly any instinct is so strong as this. Now, so many cases have been recorded of the crossed offspring from two races, neither of which are incubators, becoming first-rate sitters, that the reappearance of this instinct must be attributed to reversion from crossing. One author goes so far as to say, "that a cross between two non- {44}

sitting varieties almost invariably produces a mongrel that becomes broody, and sits with remarkable steadiness."[104] Another author, after giving a striking example, remarks that the fact can be explained only on the principle that "two negatives make a positive." It cannot, however, be maintained that hens produced from a cross between two non-sitting breeds invariably recover their lost instinct, any more than that crossed fowls or pigeons invariably recover the red or blue plumage of their prototypes. I raised several chickens from a Polish hen by a Spanish cock,—breeds which do not incubate,—and none of the young hens at first recovered their instinct, and this appeared to afford a well-marked exception to the foregoing rule; but one of these hens, the only one which was preserved, in the third year sat well on her eggs and reared a brood of chickens. So that here we have the appearance with advancing age of a primitive instinct, in the same manner as we have seen that the red plumage of the *Gallus bankiva* is sometimes reacquired by crossed and purely-bred fowls of various kinds as they grow old.

The parents of all our domesticated animals were of course aboriginally wild in disposition; and when a domesticated species is crossed with a distinct species, whether this is a domesticated or only tamed animal, the hybrids are often wild to such a degree, that the fact {45} is intelligible only on the principle that the cross has caused a partial return to the primitive disposition.

The Earl of Powis formerly imported some thoroughly domesticated humped cattle from India, and crossed them with English breeds, which belong to a distinct species; and his agent remarked to me, without any question having been asked, how oddly wild the cross-bred animals were. The European wild boar and the Chinese domesticated pig are almost certainly specifically distinct: Sir F. Darwin crossed a sow of the latter breed with a wild Alpine boar which had become extremely tame, but the young, though having half-domesticated blood in their veins, were "extremely wild in confinement, and would not eat swill like common English pigs." Mr. Hewitt, who has had great experience in crossing tame cock-pheasants with fowls belonging to five breeds, gives as the character of all "extraordinary wildness;"[105] but I have myself seen one exception to this rule. Mr. S. J. Salter,[106] who raised a large number of hybrids from a bantam-hen by *Gallus Sonneratii*, states that "all were exceedingly wild." Mr. Waterton[107] bred some wild ducks from eggs hatched under a common duck, and the young were allowed to cross freely both amongst themselves and with the tame ducks; they were "half wild and half tame; they came to the windows to be fed, but still they had a wariness about them quite remarkable."

On the other hand, mules from the horse and ass are certainly not in the least wild, yet they are notorious for obstinacy and vice. Mr. Brent, who has crossed canary-birds with many kinds of finches, has not observed, as he informs me, that the hybrids were in any way remarkably wild. Hybrids are often raised between the common and musk duck, and I have been assured by three persons, who have kept these crossed birds, that they were not wild; but Mr. Garnett[108] observed that his female hybrids exhibited "migratory propensities," of which there is not a vestige in the common or musk duck. No case is known of this latter {46} bird having escaped and become wild in Europe or Asia, except, according to Pallas, on the Caspian Sea; and the common domestic duck only occasionally becomes wild in districts where large lakes and fens abound. Nevertheless, a large number of cases have been recorded[109] of hybrids from these two ducks, although so few are reared in comparison with purely-bred birds of either species, having been shot in a completely wild state. It is improbable that any of these hybrids could have acquired their wildness from the musk-duck having paired with a truly wild duck; and this is known not to be the case in North America; hence we must infer that they have reacquired, through reversion, their wildness, as well as renewed powers of flight.

These latter facts remind us of the statements, so frequently made by travellers in all parts of the world, on the degraded state and savage disposition of crossed races of man. That many excellent and kind-hearted mulattos have existed no one will dispute; and a more mild and gentle set of men could hardly be found than the inhabitants of the island of Chiloe, who consist of Indians commingled with Spaniards in various proportions. On the other hand, many years ago, long before I had thought of the present subject, I was struck with the fact that, in South America, men of complicated descent between Negroes, Indians, and Spaniards, seldom had, whatever the cause might be, a good expression.[110] Livingstone,—and a more unimpeachable authority cannot be quoted,—after speaking of a half-caste man on the Zambesi, described by the Portuguese as a rare monster of inhumanity, remarks, "It is unaccountable why half-castes, such as he, are so much more cruel than the Portuguese, but such is undoubtedly the case." An inhabitant remarked to Livingstone, "God made white men, and God made black men, but the Devil made half-castes."[111] When two races, both low in the scale, are crossed, the progeny seems to be eminently bad. Thus the noble-hearted Humboldt, who felt none of that prejudice against the inferior races now so current in England, speaks in strong terms of the bad and savage disposition of Zambos, or half-castes between Indians and Negroes; and this conclusion has been arrived at by various observers.[112] From these facts we may perhaps infer that the degraded state of so many half-castes is in part due to reversion to a primitive and savage condition, induced by the act of crossing, as well as to the unfavourable moral conditions under which they generally exist. {47}

Summary on the proximate causes leading to Reversion.—When purely-bred animals or plants reassume long-lost characters,—when the common ass, for instance, is born with striped legs, when a pure race of black or white pigeons throws a slaty-blue bird, or when a cultivated heartsease with large and rounded flowers produces a seedling with small and elongated flowers,—we are quite unable to assign any proximate cause. When animals run wild, the tendency to reversion, which, though it has been greatly exaggerated, no doubt exists, is sometimes to a certain extent intelligible. Thus, with feral pigs, exposure to the weather will probably favour the growth of the bristles, as is known to be the case with the hair of other domesticated animals, and through correlation the tusks will tend to be redeveloped. But the reappearance of coloured longitudinal stripes on young feral pigs cannot be attributed to the direct action of external conditions. In this case, and in many others, we can only say that changed habits of life apparently have favoured a tendency, inherent or latent in the species, to return to the primitive state.

It will be shown in a future chapter that the position of flowers on the summit of the axis, and the position of seeds within the capsule, sometimes determine a tendency towards reversion; and this apparently depends on the amount of sap or nutriment which the flower-buds and seeds receive. The position, also, of buds, either on branches or on roots, sometimes determines, as was formerly shown, the transmission of the proper character of the variety, or its reversion to a former state. {48}

We have seen in the last section that when two races or species are crossed there is the strongest tendency to the reappearance in the offspring of long-lost characters, possessed by neither parent nor immediate progenitor. When two white, or red, or black pigeons, of well-established breeds, are united, the offspring are almost sure to inherit the same colours; but when differently-coloured birds are crossed, the opposed forces of inheritance apparently counteract each other, and the tendency which is inherent in both parents to produce slaty-blue offspring becomes predominant. So it is in several other cases. But when, for instance, the ass is crossed with *A. Indicus* or with the horse,—animals which have not striped legs,—and the hybrids have conspicuous stripes on their legs and even on their faces, all that can be said is, that an inherent tendency to reversion is evolved through some disturbance in the organisation caused by the act of crossing.

Another form of reversion is far commoner, indeed is almost universal with the offspring from a cross, namely, to the characters proper to either pure parent-form. As a general rule, crossed offspring in the first generation are nearly intermediate between their parents, but the grandchildren and succeeding generations continually revert, in a greater or lesser degree, to one or both of their progenitors. Several authors have maintained that hybrids and mongrels include all the characters of both parents, not fused together, but merely mingled in different proportions in different parts of the body; or, as Naudin[113] has expressed it, a hybrid is a living mosaic-work, in which the eye cannot distinguish the discordant elements, so completely are they intermingled. We can hardly doubt that, in a certain sense, this is true, as when we behold in a hybrid the elements of both species segregating themselves into segments in the same flower or fruit, by a process of self-attraction or self-affinity; this segregation taking place either by seminal or by bud-propagation. Naudin further believes that the segregation of the two specific elements or essences is eminently liable to occur in the male and female reproductive matter; and he thus explains the almost universal {49} tendency to reversion in successive hybrid generations. For this would be the natural result of the union of pollen and ovules, in both of which the elements of the same species had been segregated by self-affinity. If, on the other hand, pollen which included the elements of one species happened to unite with ovules including the elements of the other species, the intermediate or hybrid state would still be retained, and there would be no reversion. But it would, as I suspect, be more correct to say that the elements of both parent-species exist in every hybrid in a double state, namely, blended together and completely separate. How this is possible, and what the term specific essence or element may be supposed to express, I shall attempt to show in the hypothetical chapter on pangenesis.

But Naudin's view, as propounded by him, is not applicable to the reappearance of characters lost long ago by variation; and it is hardly applicable to races or species which, after having been crossed at some former period with a distinct form, and having since lost all traces of the cross, nevertheless occasionally yield an individual which reverts (as in the case of the great-great-grandchild of the pointer Sappho) to the crossing form. The most simple case of reversion, namely, of a hybrid or mongrel to its grandparents, is connected by an almost perfect series with the extreme case of a purely-bred race recovering characters which had been lost during many ages; and we are thus led to infer that all the cases must be related by some common bond.

Gärtner believed that only those hybrid plants which are highly sterile exhibit any tendency to reversion to their parent-forms. It is rash to doubt so good an observer, but this conclusion must I think be an error; and it may perhaps be accounted for by the nature of the genera observed by him, for he admits that the tendency differs in different genera. The statement is also directly contradicted by Naudin's observations, and by the notorious fact that perfectly fertile mongrels exhibit the tendency in a high degree,—even in a higher degree, according to Gärtner himself, than hybrids.[114]

Gärtner further states that reversions rarely occur with hybrid plants raised from species {50} which have not been cultivated, whilst, with those which have been long cultivated, they are of frequent occurrence. This conclusion explains a curious discrepancy: Max Wichura,[115] who worked exclusively on willows, which had not been subjected to culture, never saw an instance of reversion; and he goes so far as to suspect that the careful Gärtner had not sufficiently protected his hybrids from the pollen of the parent-species: Naudin, on the other hand, who chiefly experimented on cucurbitaceous and other cultivated plants, insists more strenuously than any other author on the tendency to reversion in all hybrids. The conclusion that the condition of the parent-species, as affected by culture, is one of the proximate causes leading to reversion, agrees fairly well with the converse case of domesticated animals and cultivated plants being liable to reversion when they become

feral; for in both cases the organisation or constitution must be disturbed, though in a very different way.

Finally, we have seen that characters often reappear in purely-bred races without our being able to assign any proximate cause; but when they become feral this is either indirectly or directly induced by the change in their conditions of life. With crossed breeds, the act of crossing in itself certainly leads to the recovery of long-lost characters, as well as of those derived from either parent-form. Changed conditions, consequent on cultivation, and the relative position of buds, flowers, and seeds on the plant, all apparently aid in giving this same tendency. Reversion may occur either through seminal or bud generation, generally at birth, but sometimes only with an advance of age. Segments or portions of the individual may alone be thus affected. That a being should be born resembling in certain characters an ancestor removed by two or three, and in some cases by hundreds or even thousands of generations, is assuredly a wonderful fact. In these cases the child is commonly said to inherit such characters directly from its grandparents or more remote ancestors. But this view is hardly conceivable. If, however, we suppose that every character is derived exclusively from the father or mother, but that many characters lie latent in both parents {51} during a long succession of generations, the foregoing facts are intelligible. In what manner characters may be conceived to lie latent, will be considered in a future chapter to which I have lately alluded.

Latent Characters.—But I must explain what is meant by characters lying latent. The most obvious illustration is afforded by secondary sexual characters. In every female all the secondary male characters, and in every male all the secondary female characters, apparently exist in a latent state, ready to be evolved under certain conditions. It is well known that a large number of female birds, such as fowls, various pheasants, partridges, peahens, ducks, &c., when old or diseased, or when operated on, partly assume the secondary male characters of their species. In the case of the hen-pheasant this has been observed to occur far more frequently during certain seasons than during others.[116] A duck ten years old has been known to assume both the perfect winter and summer plumage of the drake.[117] Waterton[118] gives a curious case of a hen which had ceased laying, and had assumed the plumage, voice, spurs, and warlike disposition of the cock; when opposed to an enemy she would erect her hackles and show fight. Thus every character, even to the instinct and manner of fighting, must have lain dormant in this hen as long as her ovaria continued to act. The females of two kinds of deer, when old, have been known to acquire horns; and, as Hunter has remarked, we see something of an analogous nature in the human species.

On the other hand, with male animals, it is notorious that the secondary sexual characters are more or less completely lost when they are subjected to castration. Thus, if the operation be performed on a young cock, he never, as Yarrell states, crows again; the comb, wattles, {52} and spurs do not grow to their full size, and the hackles assume an intermediate appearance between true hackles and the feathers of the hen. Cases are recorded of confinement alone causing analogous results. But characters properly confined to the female are likewise acquired; the capon takes to sitting on eggs, and will bring up chickens; and what is more curious, the utterly sterile male hybrids from the pheasant and the fowl act in the same manner, "their delight being to watch when the hens leave their nests, and to take on themselves the office of a sitter."[119] That admirable observer Réaumur[120] asserts that a cock, by being long confined in solitude and darkness, can be taught to take charge of young chickens; he then utters a peculiar cry, and retains during his whole life this newly acquired maternal instinct. The many well-ascertained cases of various male mammals giving milk, show that their rudimentary mammary glands retain this capacity in a latent condition.

We thus see that in many, probably in all cases, the secondary characters of each sex lie dormant or latent in the opposite sex, ready to be evolved under peculiar circumstances. We can thus understand how, for instance, it is possible for a good milking cow to transmit her good qualities through her male offspring to future generations; for we may confidently believe that these qualities are present, though latent, in the males of each generation. So it is with the game-cock, who can transmit his superiority in courage and vigour through his female to his male offspring; and with man it is known [121] that diseases, such as hydrocele, necessarily confined to the male sex, can be transmitted through the female to the grandson. Such cases as these offer, as was remarked at the commencement of this chapter, the simplest possible examples of reversion; and they are intelligible on the belief that characters common to the grandparent and grandchild of the same sex are present, though latent, in the intermediate parent of the opposite sex.

The subject of latent characters is so important, as we shall see in a future chapter, that I will give another illustration. Many animals have the right and left sides of their body {53} unequally developed: this is well known to be the case with flat-fish, in which the one side differs in thickness and colour, and in the shape of the fins, from the other; and during the growth of the young fish one eye actually travels, as shown by Steenstrup, from the lower to the upper surface.[122] In most flat-fishes the left is the blind side, but in some it is the right; though in both cases "wrong fishes," which are developed in a reversed manner to what is usual, occasionally occur, and in *Platessa flesus* the right or left side is indifferently developed, the one as often as the other. With gasteropods or shell-fish, the right and left sides are extremely unequal; the far greater number of species are dextral, with rare and occasional reversals of development, and some few are normally sinistral; but certain species of Bulimus, and, many Achatinellæ,[123] are as often sinistral as dextral. I will give an analogous case in the great Articulate kingdom: the two sides of Verruca[124] are so wonderfully unlike, that without careful dissection it is extremely difficult to recognise the corresponding parts on the opposite sides of the body; yet it is apparently a mere matter of chance whether it be the right or the left side that undergoes so singular an amount of change. One plant is known to me[125] in which the flower, according as it stands on the one or other side of the spike, is unequally developed. In all the foregoing cases the two sides of the animal are perfectly symmetrical at an early period of growth. Now, whenever a species is as liable to be unequally developed on the one as on the other side, we may infer that the capacity for such development is present, though latent, in the undeveloped side. And as a reversal of development occasionally occurs in animals of many kinds, this latent capacity is probably very common.

The best yet simplest instances of characters lying dormant are, perhaps, those previously given, in which chickens and young pigeons, raised from a cross between differently {54} coloured birds, are at first of one colour, but in a year or two acquire feathers of the colour of the other parent; for in this case the tendency to a change of plumage is clearly latent in the young bird. So it is with hornless breeds of cattle, some of which acquire, as they grow old, small horns. Purely bred black and white bantams, and some other fowls, occasionally assume, with advancing years, the red feathers of the parent-species. I will here add a somewhat different case, as it connects in a striking manner latent characters of two classes. Mr. Hewitt[126] possessed an excellent Sebright gold-laced hen bantam, which, as she became old, grew diseased in her ovaria, and assumed male characters. In this breed the males resemble the females in all respects except in their combs, wattles, spurs, and instincts; hence it might have been expected that the diseased hen would have assumed only those masculine characters which are proper to the breed, but she acquired, in addition, well-arched tail sickle-feathers quite a foot in length, saddle-feathers on the loins, and hackles on the neck,—ornaments which, as Mr. Hewitt remarks, "would be held as abominable in this breed." The Sebright bantam is known[127] to have originated about the

year 1800 from a cross between a common bantam and a Polish fowl, recrossed by a hen-tailed bantam, and carefully selected; hence there can hardly be a doubt that the sickle-feathers and hackles which appeared in the old hen were derived from the Polish fowl or common bantam; and we thus see that not only certain masculine characters proper to the Sebright bantam, but other masculine characters derived from the first progenitors of the breed, removed by a period of above sixty years, were lying latent in this hen-bird, ready to be evolved as soon as her ovaria became diseased.

From these several facts it must be admitted that certain characters, capacities, and instincts may lie latent in an individual, and even in a succession of individuals, without our being able to detect the least signs of their presence. We have already seen that the transmission of {55}
a character from the grandparent to the grandchild, with its apparent omission in the intermediate parent of the opposite sex, becomes simple on this view. When fowls, pigeons, or cattle of different colours are crossed, and their offspring change colour as they grow old, or when the crossed turbit acquired the characteristic frill after its third moult, or when purely-bred bantams partially assume the red plumage of their prototype, we cannot doubt that these qualities were from the first present, though latent, in the individual animal, like the characters of a moth in the caterpillar. Now, if these animals had produced offspring before they had acquired with advancing age their new characters, nothing is more probable than that they would have transmitted them to some of their offspring, which in this case would in appearance have received such characters from their grandparents or more distant progenitors. We should then have had a case of reversion, that is, of the reappearance in the child of an ancestral character, actually present, though during youth completely latent, in the parent; and this we may safely conclude is what occurs with reversions of all kinds to progenitors however remote.

This view of the latency in each generation of all the characters which appear through reversion, is also supported by their actual presence in some cases during early youth alone, or by their more frequent appearance and greater distinctness at this age than during maturity. We have seen that this is often the case with the stripes on the legs and faces of the several species of the horse-genus. The Himalayan rabbit, when crossed, sometimes produces offspring which revert to the parent silver-grey breed, and we have seen that in purely bred animals pale-grey fur occasionally reappears during early youth. Black cats, we may feel assured, would occasionally produce by reversion tabbies; and on young black kittens, with a pedigree[128] known to have been long pure, faint traces of stripes may almost always be seen which afterwards disappear. Hornless Suffolk cattle occasionally produce by reversion horned animals; and Youatt[129] asserts that even in hornless individuals "the rudiment of a horn may be often felt at an early age." {56}

No doubt it appears at first sight in the highest degree improbable that in every horse of every generation there should be a latent capacity and tendency to produce stripes, though these may not appear once in a thousand generations; that in every white, black, or other coloured pigeon, which may have transmitted its proper colour during centuries, there should be a latent capacity in the plumage to become blue and to be marked with certain characteristic bars; that in every child in a six-fingered family there should be the capacity for the production of an additional digit; and so in other cases. Nevertheless there is no more inherent improbability in this being the case than in a useless and rudimentary organ, or even in only a tendency to the production of a rudimentary organ, being inherited during millions of generations, as is well known to occur with a multitude of organic beings. There is no more inherent improbability in each domestic pig, during a thousand generations, retaining the capacity and tendency to develop great tusks under fitting conditions, than in the young calf having retained for an indefinite number of generations rudimentary incisor teeth, which never protrude through the gums.

I shall give at the end of the next chapter a summary of the three preceding chapters; but as isolated and striking cases of reversion have here been chiefly insisted on, I wish to guard the reader against supposing that reversion is due to some rare or accidental combination of circumstances. When a character, lost during hundreds of generations, suddenly reappears, no doubt some such combination must occur; but reversions may be constantly observed, at least to the immediately preceding generations, in the offspring of most unions. This has been universally recognised in the case of hybrids and mongrels, but it has been recognised simply from the difference between the united forms rendering the resemblance of the offspring to their grandparents or more remote progenitors of easy detection. Reversion is likewise almost invariably the rule, as Mr. Sedgwick has shown, with certain diseases. Hence we must conclude that a tendency to this peculiar form of transmission is an integral part of the general law of inheritance. {57}

Monstrosities.—A large number of monstrous growths and of lesser anomalies are admitted by every one to be due to an arrest of development, that is to the persistence of an embryonic condition. If every horse or ass had striped legs whilst young, the stripes which occasionally appear on these animals when adult would have to be considered as due to the anomalous retention of an early character, and not as due to reversion. Now, the leg-stripes in the horse-genus, and some other characters in analogous cases, are apt to occur during early youth and then to disappear; thus the persistence of early characters and reversion are brought into close connexion.

But many monstrosities can hardly be considered as the result of an arrest of development; for parts of which no trace can be detected in the embryo, but which occur in other members of the same class of animals or plants, occasionally appear, and these may probably with truth be attributed to reversion. For instance: supernumerary mammæ, capable of secreting milk, are not extremely rare in women; and as many as five have been observed. When four are developed, they are generally arranged symmetrically on each side of the chest; and in one instance a woman (the daughter of another with supernumerary mammæ) had one mamma, which yielded milk, developed in the inguinal region. This latter case, when we remember the position of the mammæ in some of the lower animals on both the chest and inguinal region, is highly remarkable, and leads to the belief that in all cases the additional mammæ in woman are due to reversion. The facts given in the last chapter on the tendency in supernumerary digits to regrowth after amputation, indicate their relation to the digits of the lower vertebrate animals, and lead to the suspicion that their appearance may in some manner be connected with reversion. But I shall have to recur, in the chapter on pangenesis, to the abnormal multiplication of organs, and likewise to their occasional transposition. The occasional development in man of the coccygeal vertebræ into a short and free tail, though it thus becomes in one sense more perfectly developed, may at the same time be considered as an arrest of development, and as a case of reversion. The greater frequency of a monstrous kind of proboscis in the pig than in any other mammal, considering the position of the pig in the mammalian series, has likewise been attributed, perhaps truly, to reversion. {58} [130]

> When flowers which are properly irregular in structure become regular or peloric, the change is generally looked at by botanists as a return to the primitive state. But Dr. Maxwell Masters,[131] who has ably discussed this subject, remarks that when, for instance, all the sepals of a Tropæolum become green and of the same shape, instead of being coloured with one alone prolonged into a spur, or when all the petals of a Linaria become simple and regular, such cases may be due merely to an arrest of development; for in these flowers all the organs during their earliest condition are symmetrical, and, if arrested at this stage of growth, they would not become irregular. If, moreover, the arrest were to take place at a still earlier period of development, the result would be a simple tuft of green leaves; and no one probably would call this a

case of reversion. Dr. Masters designates the cases first alluded to as regular peloria; and others, in which all the corresponding parts assume a similar form of irregularity, as when all the petals in a Linaria become spurred, as irregular peloria. We have no right to attribute these latter cases to reversion, until it can be shown to be probable that the parent-form, for instance, of the genus Linaria had had all its petals spurred; for a change of this nature might result from the spreading of an anomalous structure, in accordance with the law, to be discussed in a future chapter, of homologous parts tending to vary in the same manner. But as both forms of peloria frequently occur on the same individual plant of the Linaria,[132] they probably stand in some close relation to each other. On the doctrine that peloria is simply the result of an arrest of development, it is difficult to understand how an organ arrested at a very early period of growth should acquire its full functional perfection;—how a petal, supposed to be thus arrested, should acquire its brilliant colours, and serve as an envelope to the flower, or a stamen produce efficient pollen; yet this occurs with many peloric flowers. That pelorism is not due to mere chance variability, but either to an arrest of development or to reversion, we may infer from an observation made by Ch. Morren, [133] namely, that families which have irregular flowers often "return by these monstrous growths to their regular form; whilst we never see a regular flower realise the structure of an irregular one."

Some flowers have almost certainly become more or less completely peloric through reversion. *Corydalis tuberosa* properly has one of its two nectaries colourless, destitute of nectar, only half the size of the other, and therefore, to a certain extent, in a rudimentary state; the pistil is curved towards the perfect nectary, and the hood, formed of the inner petals, slips off the pistil and stamens in one direction alone, so that, when a bee sucks the perfect nectary, the stigma and stamens are exposed and rubbed against the insect's body. In several closely allied genera, as in Dielytra, &c., there are two perfect nectaries, the pistil is straight, and the hood slips off on either side, according as the bee sucks either nectary. Now, I have examined several flowers of *Corydalis tuberosa*, in which both nectaries were equally developed and contained nectar; in this we see only the redevelopment of a partially aborted organ; but with this redevelopment the pistil becomes straight, and the hood slips off in either direction; so that these flowers have acquired the perfect structure, so well adapted for insect agency, of Dielytra and its allies. We cannot attribute these coadapted modifications to chance, or to correlated variability; we must attribute them to reversion to a primordial condition of the species. {59}

The peloric flowers of Pelargonium have their five petals in all respects alike, and there is no nectary; so that they resemble the symmetrical flowers of the closely allied Geranium-genus; but the alternate stamens are also sometimes destitute of anthers, the shortened filaments being left as rudiments, and in this respect they resemble the symmetrical flowers of the closely allied genus, Erodium. Hence we are led to look at the peloric flowers of Pelargonium as having probably reverted to the state of some primordial form, the progenitor of the three closely related genera of Pelargonium, Geranium, and Erodium.

In the peloric form of *Antirrhinum majus*, appropriately called the "*Wonder*," the tubular and elongated flowers differ wonderfully from those of the common snapdragon; the calyx and the mouth of the corolla consist of six equal lobes, and include six equal instead of four unequal stamens. One of the two additional stamens is manifestly formed by the development of a microscopically minute papilla, which may be found at the base of the upper lip of the flower in all common snapdragons, at least in nineteen plants examined by me. That this papilla is a rudiment of a stamen was well shown by its various degrees of development in crossed plants between the common and peloric Antirrhinum. Again, a peloric *Galeobdolon luteum*, growing in

my garden, had five equal petals, all striped like the ordinary lower lip, and included five equal instead of four unequal stamens; but Mr. R. Keeley, who sent me this plant, informs me that the flowers vary greatly, having from four to six lobes to the corolla, and from three to six stamens.[134] Now, as the members of the two great families to which the Antirrhinum and Galeobdolon belong are properly pentamerous, with some of the parts confluent and others suppressed, we ought not to look at the sixth stamen and the sixth lobe to the corolla in either case as due to reversion, any more than the additional petals in double flowers in these same two families. But the case is different with the fifth stamen in the peloric Antirrhinum, which is produced by the redevelopment of a rudiment always present, and which probably reveals to us the state of the flower, as far as the stamens are concerned, at some ancient epoch. It is also difficult to believe that the other four stamens and the petals, after an arrest of development at a very early embryonic age, would have come to full perfection in colour, structure, and function, unless these organs had at some former period normally passed through a similar course of growth. Hence it appears to me probable that the progenitor of the genus Antirrhinum must at some remote epoch have included five stamens and borne flowers in some degree resembling those now produced by the peloric form. {60}

Lastly, I may add that many instances have been recorded of flowers, not generally ranked as peloric, in which certain organs, normally few in number, have been abnormally augmented. As such an increase of parts cannot be looked at as an arrest of development, nor as due to the redevelopment of rudiments, for no rudiments are present, and as these additional parts bring the plant into closer relationship with its natural allies, they ought probably to be viewed as reversions to a primordial condition.

These several facts show us in an interesting manner how intimately certain abnormal states are connected together; namely, arrests of development causing parts to become rudimentary or to be wholly suppressed,—the redevelopment of parts at present in a more or less rudimentary condition,—the reappearance of organs of which not a vestige can now be detected,—and to these may be added, in the case of animals, the presence during youth, and subsequent disappearance, of certain characters which occasionally are retained throughout life. Some naturalists look at all such abnormal structures as a return to the ideal state of the group to which the affected being belongs; but it is difficult to conceive what is meant to be conveyed by this expression. Other naturalists maintain, with greater probability and distinctness of view, that the common bond of connection between the several foregoing cases is an actual, though partial, return to the structure of the ancient progenitor of the group. If this view be correct, we must believe that a vast number of characters, capable of evolution, lie hidden in every organic being. But it would be a mistake to suppose that the number is equally great in all beings. We know, for instance, that plants of many orders occasionally become peloric; but many more cases have been observed in the Labiatæ and Scrophulariaceæ than in any other order; and in one genus of the Scrophulariaceæ, namely Linaria, no less than thirteen species have been described in a peloric condition.[135] On this view of the nature of peloric flowers, and bearing in mind what has been said with respect to certain monstrosities in the animal kingdom, we must conclude that the progenitors of most plants and animals, though widely different in structure, have left an impression capable of redevelopment on the germs of their descendants. {61}

The fertilised germ of one of the higher animals, subjected as it is to so vast a series of changes from the germinal cell to old age,—incessantly agitated by what Quatrefages well calls the *tourbillon vital*,—is perhaps the most wonderful object in nature. It is probable that hardly a change of any kind affects either parent, without some mark being left on the germ.

But on the doctrine of reversion, as given in this chapter, the germ becomes a far more marvellous object, for, besides the visible changes to which it is subjected, we must believe that it is crowded with invisible characters, proper to both sexes, to both the right and left side of the body, and to a long line of male and female ancestors separated by hundreds or even thousands of generations from the present time; and these characters, like those written on paper with invisible ink, all lie ready to be evolved under certain known or unknown conditions.

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CHAPTER XIV.

INHERITANCE *continued*—FIXEDNESS OF CHARACTER—PREPOTENCY—SEXUAL LIMITATION—CORRESPONDENCE OF AGE.

FIXEDNESS OF CHARACTER APPARENTLY NOT DUE TO ANTIQUITY OF INHERITANCE—PREPOTENCY OF TRANSMISSION IN INDIVIDUALS OF THE SAME FAMILY, IN CROSSED BREEDS AND SPECIES; OFTEN STRONGER IN ONE SEX THAN THE OTHER; SOMETIMES DUE TO THE SAME CHARACTER BEING PRESENT AND VISIBLE IN ONE BREED AND LATENT IN THE OTHER—INHERITANCE AS LIMITED BY SEX—NEWLY-ACQUIRED CHARACTERS IN OUR DOMESTICATED ANIMALS OFTEN TRANSMITTED BY ONE SEX ALONE, SOMETIMES LOST BY ONE SEX ALONE—INHERITANCE AT CORRESPONDING PERIODS OF LIFE—THE IMPORTANCE OF THE PRINCIPLE WITH RESPECT TO EMBRYOLOGY; AS EXHIBITED IN DOMESTICATED ANIMALS; AS EXHIBITED IN THE APPEARANCE AND DISAPPEARANCE OF INHERITED DISEASES; SOMETIMES SUPERVENING EARLIER IN THE CHILD THAN IN THE PARENT—SUMMARY OF THE THREE PRECEDING CHAPTERS.

In the two last chapters the nature and force of Inheritance, the circumstances which interfere with its power, and the tendency to Reversion, with its many remarkable contingencies, were discussed. In the present chapter some other related phenomena will be treated of, as fully as my materials permit.

Fixedness of Character.

It is a general belief amongst breeders that the longer any character has been transmitted by a breed, the more firmly it will continue to be transmitted. I do not wish to dispute the truth of the proposition, that inheritance gains strength simply through long continuance, but I doubt whether it can be proved. In one sense the proposition is little better than a truism; if any character has remained constant during many generations, it will obviously be little likely, the conditions of life remaining the same, to vary during the next generation. So, again, in improving a breed, if care be taken for a length of time to exclude all inferior individuals, the breed will obviously tend to become truer, as it will not have been crossed during many generations by an inferior animal. We have previously seen, but without being {63} able to assign any cause, that, when a new character appears, it is occasionally from the first well fixed, or fluctuates much, or wholly fails to be transmitted. So it is with the aggregate of slight differences which characterise a new variety, for some propagate their kind from the first much truer than others. Even with plants multiplied by bulbs, layers, &c., which may in one sense be said to form parts of the same individual, it is well known that certain varieties retain and transmit through successive bud-generations their newly-acquired characters more truly than others. In none of these, nor in the following cases, does there appear to be any relation between the force with which a character is transmissible and the length of time during which it has already been transmitted. Some varieties, such as white and yellow hyacinths and white sweet-peas, transmit their colours more faithfully than do the varieties which have retained their natural colour. In the Irish family, mentioned in the twelfth chapter, the peculiar tortoiseshell-like colouring of the eyes was transmitted far

more faithfully than any ordinary colour. Ancon and Mauchamp sheep and niata cattle, which are all comparatively modern breeds, exhibit remarkably strong powers of inheritance. Many similar cases could be adduced.

As all domesticated animals and cultivated plants have varied, and yet are descended from aboriginally wild forms, which no doubt had retained the same character from an immensely remote epoch, we see that scarcely any degree of antiquity ensures a character being transmitted perfectly true. In this case, however, it may be said that changed conditions of life induce certain modifications, and not that the power of inheritance fails; but in every case of failure, some cause, either internal or external, must interfere. It will generally be found that the parts in our domesticated productions which have varied, or which still continue to vary,—that is, which fail to retain their primordial state,—are the same with the parts which differ in the natural species of the same genus. As, on the theory of descent with modification, the species of the same genus have been modified since they branched off from a common progenitor, it follows that the characters by which they differ from each other have varied whilst other parts of the organisation have remained unchanged; and it might be argued that these same characters now vary under {64} domestication, or fail to be inherited, owing to their lesser antiquity. But we must believe structures, which have already varied, would be more liable to go on varying, rather than structures which during an immense lapse of time have remained unaltered; and this variation is probably the result of certain relations between the conditions of life and the organisation, quite independently of the greater or less antiquity of each particular character.

Fixedness of character, or the strength of inheritance, has often been judged of by the preponderance of certain characters in the crossed offspring between distinct races; but prepotency of transmission here comes into play, and this, as we shall immediately see, is a very different consideration from the strength or weakness of inheritance. It has often been observed[136] that breeds of animals inhabiting wild and mountainous countries cannot be permanently modified by our improved breeds; and as these latter are of modern origin, it has been thought that the greater antiquity of the wilder breeds has been the cause of their resistance to improvement by crossing; but it is more probably due to their structure and constitution being better adapted to the surrounding conditions. When plants are first subjected to culture, it has been found that, during several generations, they transmit their characters truly, that is, do not vary, and this has been attributed to ancient characters being strongly inherited; but it may with equal or greater probability be consequent on changed conditions of life requiring a long time for their accumulative action. Notwithstanding these considerations, it would perhaps be rash to deny that characters become more strongly fixed the longer they are transmitted; but I believe that the proposition resolves itself into this,—that all characters of all kinds, whether new or old, tend to be inherited, and that those which have already withstood all counteracting influences and been truly transmitted, will, as a general rule, continue to withstand them, and consequently be faithfully inherited.

Prepotency in the Transmission of Character. {65}

When individuals distinct enough to be recognised, but of the same family, or when two well-marked races, or two species, are crossed, the usual result, as stated in the previous chapter, is, that the offspring in the first generation are intermediate between their parents, or resemble one parent in one part and the other parent in another part. But this is by no means the invariable rule; for in many cases it is found that certain individuals, races, and species are prepotent in transmitting their likeness. This subject has been ably discussed by Prosper Lucas,[137] but is rendered extremely complicated by the prepotency sometimes running equally in both sexes, and sometimes more strongly in one sex than in the other; it is likewise complicated by the presence of secondary sexual characters, which render the comparison of mongrels with their parent-breeds difficult.

It would appear that in certain families some one ancestor, and after him others in the same family, must have had great power in transmitting their likeness through the male line; for we cannot otherwise understand how the same features should so often be transmitted after marriages with various females, as has been the case with the Austrian Emperors, and as, according to Niebuhr, formerly occurred in certain Roman families with their mental qualities.[138] The famous bull Favourite is believed[139] to have had a prepotent influence on the shorthorn race. It has also been observed[140] with English race-horses that certain mares have generally transmitted their own character, whilst other mares of equally pure blood have allowed the character of the sire to prevail.

The truth of the principle of prepotency comes out more clearly when certain races are crossed. The improved Shorthorns, notwithstanding that the breed is comparatively modern, are generally acknowledged to possess great power in impressing their likeness on all other breeds; and it is chiefly in consequence of this power that they are so highly valued for exportation.[141] Godine has given a curious case of a ram of {66} 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. Girou de Buzareingues[142] found that of two races of French sheep the ewes of one, when crossed during successive generations with merino rams, yielded up their character far sooner than the ewes of the other race. Sturm and Girou have given analogous cases with other breeds of sheep and with cattle, the prepotency running in these cases through the male side; but I was assured on good authority in South America, that when niata cattle are crossed with common cattle, though the niata breed is prepotent whether males or females are used, yet that the prepotency is strongest through the female line. The Manx cat is tailless and has long hind legs; Dr. Wilson crossed a male Manx 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.[143]

In making reciprocal crosses between pouter and fantail pigeons, the pouter-race seemed to be prepotent through both sexes over the fantail. But this is probably due to weak power in the fantail rather than to any unusually strong power in the pouter, for I have observed that barbs also preponderated over fantails. This weakness of transmission in the fantail, though the breed is an ancient one, is said[144] to be general; but I have observed one exception to the rule, namely, in a cross between a fantail and laugher. The most curious instance known to me of weak power in both sexes is in the trumpeter pigeon. This breed has been well known for at least 130 years: it breeds perfectly true, as I have been assured by those who have long kept many birds: it is characterised by a peculiar tuft of feathers over the beak, by a crest on the head, by a most peculiar coo quite unlike that of any other breed, and by much-feathered feet. I have crossed both sexes with turbits of two sub-breeds, with almond tumblers, spots, and runts, and reared many mongrels and recrossed them; and though the crest on the head and feathered feet were inherited (as is generally the case with most breeds), I have never seen a vestige of the tuft over the beak or heard the peculiar coo. Boitard and Corbié[145] assert that this is the invariable result of crossing trumpeters with any other breed: Neumeister,[146] however, states that in Germany mongrels have been obtained, though very rarely, which were furnished with the tuft and would trumpet: but a pair of these mongrels with a tuft, which I imported, never trumpeted. Mr. Brent states[147] that the crossed offspring of a trumpeter were crossed with trumpeters for three generations, by which time the mongrels had 7-8ths of this {67}

blood in their veins, yet the tuft over the beak did not appear. At the fourth generation the tuft appeared, but the birds, though now having 15-16ths trumpeter's blood, still did not trumpet. This case well shows the wide difference between inheritance and prepotency; for here we have a well-established old race which transmits it characters faithfully, but which, when crossed with any other race, has the feeblest power of transmitting its two chief characteristic qualities.

I will give one other instance with fowls and pigeons of weakness and strength in the transmission of the same character to their crossed offspring. The Silk-fowl breeds true, and there is reason to believe 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.[148] So that it is certain that this breed very seldom has the power of transmitting its peculiar plumage to its crossed progeny. On the other hand, there is a silk sub-variety of the fantail pigeon, which has its feathers in nearly the same state as in the Silk-fowl: now we have already seen that fantails, when crossed, possess singularly weak power in transmitting their general qualities; but the silk sub-variety when crossed with any other small-sized race invariably transmits its silky feathers! [149]

The law of prepotency comes into action when species are crossed, as with races and individuals. Gärtner has unequivocally shown[150] that this is the case with plants. To give one instance: when *Nicotiana paniculata* and *vincæflora* are crossed, the character of *N. paniculata* is almost completely lost in the hybrid; but if *N. quadrivalvis* be crossed with *N. vincæflora*, this later species, which was before so prepotent, now in its turn almost disappears under the power of *N. quadrivalvis*. It is remarkable that the prepotency of one species over another in transmission is quite independent, as shown by Gärtner, of the greater or less facility with which the one fertilises the other.

With animals, the jackal is prepotent over the dog, as is stated by Flourens who made many crosses between these animals; and this was likewise the case with a hybrid which I once saw between a jackal and terrier. I cannot doubt, from the observations of Colin and others, that the ass is prepotent over the horse; the prepotency in this instance running more strongly through the male than through the female ass; so that the mule resembles the ass more closely than does the hinny.[151] The male pheasant, {68} judging from Mr. Hewitt's descriptions,[152] and from the hybrids which I have seen, preponderates over the domestic fowl; but the latter, as far as colour is concerned, has considerable power of transmission, for hybrids raised from five differently coloured hens differed greatly in plumage. I formerly examined some curious hybrids in the Zoological Gardens, between the Penguin variety of the common duck and the Egyptian goose (*Tadorna Ægyptiaca*); and although I will not assert that the domesticated variety preponderated over the natural species, yet it had strongly impressed its unnatural upright figure on these hybrids.

I am aware that such cases as the foregoing have been ascribed by various authors, not to one species, race, or individual being prepotent over the other in impressing it character on its crossed offspring, but to such rules as that the father influences the external characters and the mother the internal or vital organs. But the great diversity of the rules given by various authors almost proves their falseness. Dr. Prosper Lucas has fully discussed this point, and has shown[153] that none of the rules (and I could add others to those quoted by him) apply to all animals. Similar rules have been

enounced for plants, and have been proved by Gärtner[154] to be all erroneous. If we confine our view to the domesticated races of a single species, or perhaps even to the species of the same genus, some such rules may hold good; for instance, it seems that in reciprocally crossing various breeds of fowls the male generally gives colour;[155] but conspicuous exceptions have passed under my own eyes. In sheep it seems that the ram usually gives its peculiar horns and fleece to its crossed offspring, and the bull the presence or absence of horns.

In the following chapter on Crossing I shall have occasion to show that certain characters are rarely or never blended by crossing, but are transmitted in an unmodified state from either parent-form; I refer to this fact here because it is sometimes accompanied on the one side by prepotency, which thus acquires the false appearance of unusual strength. In the same chapter I shall show that the rate at which a species or breed absorbs and obliterates another by repeated crosses, depends in chief part on prepotency in transmission. {69}

In conclusion, some of the cases above given,—for instance, that of the trumpeter pigeon,—prove that there is a wide difference between mere inheritance and prepotency. This latter power seems to us, in our ignorance, to act in most cases quite capriciously. The very same character, even though it be an abnormal or monstrous one, such as silky feathers, may be transmitted by different species, when crossed, either with prepotent force or singular feebleness. It is obvious, that a purely-bred form of either sex, in all cases in which prepotency does not run more strongly in one sex than the other, will transmit its character with prepotent force over a mongrelized and already variable form.[156] From several of the above-given cases we may conclude that mere antiquity of character does not by any means necessarily make it prepotent. In some cases prepotency apparently depends on the same character being present and visible in one of the two breeds which are crossed, and latent or invisible in the other breed; and in this case it is natural that the character which is potentially present in both should be prepotent. Thus, we have reason to believe that there is a latent tendency in all horses to be dun-coloured and striped; and when a horse of this kind is crossed with one of any other colour, it is said that the offspring are almost sure to be striped. Sheep have a similar latent tendency to become dark-coloured, and we have seen with what prepotent force a ram with a few black spots, when crossed with sheep of various breeds, coloured its offspring. All pigeons have a latent tendency to become slaty-blue, with certain characteristic marks, and it is known that, when a bird thus coloured is crossed with one of any other colour, it is most difficult afterwards to eradicate the blue tint. A nearly parallel case is offered by those black bantams which, as they grow old, develop a latent tendency to acquire red feathers. But there are exceptions to the rule: hornless breeds of cattle possess a latent capacity to reproduce horns, yet when crossed with horned breeds they do not invariably produce offspring bearing horns. {70}

We meet with analogous cases with plants. Striped flowers, though they can be propagated truly by seed, have a latent tendency to become uniformly coloured, but when once crossed by a uniformly coloured variety, they ever afterwards fail to produce striped seedlings.[157] Another case is in some respects more curious: plants bearing peloric or regular flowers have so strong a latent tendency to reproduce their normally irregular flowers, that this often occurs by buds when a plant is transplanted into poorer or richer soil.[158] Now I crossed the peloric snapdragon (*Antirrhinum majus*), described in the last chapter, with pollen of the common form; and the latter, reciprocally, with peloric pollen. I thus raised two great beds of seedlings, and not one was peloric. Naudin[159] obtained the same result from crossing a peloric Linaria with the common form. I carefully examined the flowers of ninety plants of the crossed Antirrhinum in the two beds, and their structure had not been in the least affected by the cross, except that in a few instances the minute rudiment of the fifth stamen,

which is always present, was more fully or even completely developed. It must not be supposed that this entire obliteration of the peloric structure in the crossed plants can be accounted for by any incapacity of transmission; for I raised a large bed of plants from the peloric Antirrhinum, artificially fertilised by its own pollen, and sixteen plants, which alone survived the winter, were all as perfectly peloric as the parent-plant. Here we have a good instance of the wide difference between the inheritance of a character and the power of transmitting it to crossed offspring. The crossed plants, which perfectly resembled the common snapdragon, were allowed to sow themselves, and, out of a hundred and twenty-seven seedlings, eighty-eight proved to be common snapdragons, two were in an intermediate condition between the peloric and normal state, and thirty-seven were perfectly {71}
peloric, having reverted to the structure of their one grandparent. This case seems at first sight to offer an exception to the rule formerly given, namely, that a character which is present in one form and latent in the other is generally transmitted with prepotent force when the two forms are crossed. For in all the Scrophulariaceæ, and especially in the genera Antirrhinum and Linaria, there is, as was shown in the last chapter, a strong latent tendency to become peloric; and there is also, as we have just seen, a still stronger tendency in all peloric plants to reacquire their normal irregular structure. So that we have two opposed latent tendencies in the same plants. Now, with the crossed Antirrhinums the tendency to produce normal or irregular flowers, like those of the common Snapdragon, prevailed in the first generation; whilst the tendency to pelorism, appearing to gain strength by the intermission of a generation, prevailed to a large extent in the second set of seedlings. How it is possible for a character to gain strength by the intermission of a generation, will be considered in the chapter on pangenesis.

On the whole, the subject of prepotency is extremely intricate,—from its varying so much in strength, even in regard to the same character, in different animals,—from its running either equally in both sexes, or, as frequently is the case with animals, but not with plants, much stronger in the one sex than the other,—from the existence of secondary sexual characters,—from the transmission of certain characters being limited, as we shall immediately see, by sex,—from certain characters not blending together,—and, perhaps, occasionally from the effects of a previous fertilisation on the mother. It is therefore not surprising that every one hitherto has been baffled in drawing up general rules on the subject of prepotency.

Inheritance as limited by Sex.

New characters often appear in one sex, and are afterwards transmitted to the same sex, either exclusively or in a much greater degree than to the other. This subject is important, because with animals of many kinds in a state of nature, both high and low in the scale, secondary sexual characters, not in any way directly connected with the organs of {72}
reproduction, are often conspicuously present. With our domesticated animals, also, these same secondary characters are often found to differ greatly from the state in which they exist in the parent-species. And the principle of inheritance as limited by sex shows how such characters might have been first acquired and subsequently modified.

> Dr. P. Lucas, who has collected many facts on this subject, shows[160] that when a peculiarity, in no manner connected with the reproductive organs, appears in either parent, it is often transmitted exclusively to the offspring of the same sex, or to a much greater number of them than of the opposite sex. Thus, in the family of Lambert, the horn-like projections on the skin were transmitted from the father to his sons and grandsons alone; so it has been with other cases of ichthyosis, with supernumerary digits, with a deficiency of digits and phalanges, and in a lesser degree with various diseases, especially with colour-blindness, and a hæmorrhagic diathesis, that is, an extreme liability to profuse and uncontrollable bleeding from trifling wounds. On the other hand, mothers have transmitted, during several generations, to their daughters alone, supernumerary and deficient digits, colour-blindness, and other

peculiarities. So that we see that the very same peculiarity may become attached to either sex, and be long inherited by that sex alone; but the attachment in certain cases is much more frequent to one than the other sex. The same peculiarities also may be promiscuously transmitted to either sex. Dr. Lucas gives other cases, showing that the male occasionally transmits his peculiarities to his daughters alone, and the mother to her sons alone; but even in this case we see that inheritance is to a certain extent, though inversely, regulated by sex. Dr. Lucas, after weighing the whole evidence, comes to the conclusion that every peculiarity, according to the sex in which it first appears, tends to be transmitted in a greater or lesser degree to that sex.

A few details from the many cases collected by Mr. Sedgwick,[161] may be here given. Colour-blindness, from some unknown cause, shows itself much oftener in males than in females; in upwards of two hundred cases collected by Mr. Sedgwick, nine-tenths related to men; but it is eminently liable to be transmitted through women. In the case given by Dr. Earle, members of eight related families were affected during five generations: these families consisted of sixty-one individuals, namely, of thirty-two males, of whom nine-sixteenths were incapable of distinguishing colour, and of twenty-nine females, of whom only one-fifteenth were thus affected. Although colour-{73} blindness thus generally clings to the male sex, nevertheless, in one instance in which it first appeared in a female, it was transmitted during five generations to thirteen individuals, all of whom were females. A hæmorrhagic diathesis, often accompanied by rheumatism, has been known to affect the males alone during five generations, being transmitted, however, through the females. It is said that deficient phalanges in the fingers have been inherited by the females alone during ten generations. In another case, a man thus deficient in both hands and feet, transmitted the peculiarity to his two sons and one daughter; but in the third generation, out of nineteen grandchildren, twelve sons had the family defect, whilst the seven daughters were free. In ordinary cases of sexual limitation, the sons or daughters inherit the peculiarity, whatever it may be, from their father or mother, and transmit it to their children of the same sex; but generally with the hæmorrhagic diathesis, and often with colour-blindness, and in some other cases, the sons never inherit the peculiarity directly from their fathers, but the daughters, and the daughters alone, transmit the latent tendency, so that the sons of the daughters alone exhibit it. Thus, the father, grandson, and great-great-grandson will exhibit a peculiarity,—the grandmother, daughter, and great-granddaughter having transmitted it in a latent state. Hence we have, as Mr. Sedgwick remarks, a double kind of atavism or reversion; each grandson apparently receiving and developing the peculiarity from his grandfather, and each daughter apparently receiving the latent tendency from her grandmother.

From the various facts recorded by Dr. Prosper Lucas, Mr. Sedgwick, and others, there can be no doubt that peculiarities first appearing in either sex, though not in any way necessarily or invariably connected with that sex, strongly tend to be inherited by the offspring of the same sex, but are often transmitted in a latent state through the opposite sex.

Turning now to domesticated animals, we find that certain characters not proper to the parent-species are often confined to, and inherited by, one sex alone; but we do not know the history of the first appearance of such characters. In the chapter on Sheep, we have seen that the males of certain races differ greatly from the females in the shape of their horns, these being absent in the ewes of some breeds, in the development of fat in the tail in certain fat-tailed breeds, and in the outline of the forehead. These differences, judging from the character of the allied wild species, cannot be accounted for by supposing that they have been derived from distinct parent-forms. There is, also, a great difference between the horns of the two sexes in one Indian breed of goats. The bull zebu is said to have a larger hump than the cow. In

the Scotch deer-hound the two sexes differ in size more than in any other variety of the dog,[162] and, judging from analogy, more than in the aboriginal parent-species. The peculiar colour called tortoise-shell is very rarely seen in a male cat; the males of this variety being of a rusty tint. A tendency to baldness in man before the advent of old age is certainly inherited; and in the European, or at least in the Englishman, is an attribute of the male sex, and may almost be ranked as an incipient secondary sexual character. {74}

In various breeds of the fowl the males and females often differ greatly; and these differences are far from being the same with those which distinguish the two sexes in the parent-species, the *Gallus bankiva*; and consequently have originated under domestication. In certain sub-varieties of the Game race we have the unusual case of the hens differing from each other more than the cocks. In an Indian breed of a white colour stained with soot, the hens invariably have black skins, and their bones are covered by a black periosteum, whilst the cocks are never or most rarely thus characterised. Pigeons offer a more interesting case; for the two sexes rarely differ throughout the whole great family, and the males and females of the parent-form, the *C. livia*, are undistinguishable; yet we have seen that with Pouters the male has the characteristic quality of pouting more strongly developed than the female; and in certain sub-varieties[163] the males alone are spotted or striated with black. When male and female English carrier-pigeons are exhibited in separate pens, the difference in the development of the wattle over the beak and round the eyes is conspicuous. So that here we have instances of the appearance of secondary sexual characters in the domesticated races of a species in which such differences are naturally quite absent.

On the other hand, secondary sexual characters which properly belong to the species are sometimes quite lost, or greatly diminished, under domestication. We see this in the small size of the tusks in our improved breeds of the pig, in comparison with those of the wild boar. There are sub-breeds of fowls in which the males have lost the fine flowing tail-feathers and hackles; and others in which there is no difference in colour between the two sexes. In some cases the barred plumage, which in gallinaceous birds is commonly the attribute of the hen, has been transferred to the cock, as in the cuckoo sub-breeds. In other cases masculine characters have been partly transferred to the female, as with the splendid plumage of the golden-spangled Hamburgh hen, the enlarged comb of the Spanish hen, the pugnacious disposition of the Game hen, and as in the well-developed spurs which occasionally appear in the hens of various breeds. In Polish fowls both sexes are ornamented with a topknot, that of the male being formed of hackle-like feathers, and this is a new male character in the genus Gallus. On the whole, as far as I can judge, new characters are more apt to appear in the males of our domesticated animals than in the females, and afterwards to be either exclusively or more strongly inherited by the males. Finally, in accordance with the principle of inheritance as limited by sex, the appearance of secondary sexual characters in natural species offers no especial difficulty, and their subsequent increase and modification, if of any service to the species, would follow through that form of selection which in my 'Origin of Species' I have called sexual selection. {75}

Inheritance at corresponding periods of Life.

This is an important subject. Since the publication of my 'Origin of Species,' I have seen no reason to doubt the truth of the explanation there given of perhaps the most remarkable of all the facts in biology, namely, the difference between the embryo and the adult animal. The explanation is, that variations do not necessarily or generally occur at a very early period of embryonic growth, and that such variations are inherited at a corresponding age. As a consequence of this the embryo, even when the parent-form undergoes a great amount of modification, is left only slightly modified; and the embryos of widely-different animals

which are descended from a common progenitor remain in many important respects like each other and their common progenitor. We can thus understand why embryology should throw a flood of light on the natural system of classification, for this ought to be as far as possible genealogical. When the embryo leads an independent life, that is, becomes a larva, it has to be adapted to the surrounding conditions in its structure and instincts, independently of those of its parents; and the principle of inheritance at corresponding periods of life renders this possible.

This principle is, indeed, in one way so obvious that it escapes attention. We possess a number of races of animals and plants, which, when compared with each other and with their parent-forms, present conspicuous differences, both in the immature and mature states. Look at the seeds of the several kinds of peas, beans, maize, which can be propagated truly, and see how they differ in size, colour, and shape, whilst the full-grown plants differ but little. Cabbages on the other hand differ greatly in foliage and manner of growth, but hardly at all in their seeds; and generally it will be found that the differences between cultivated plants at different periods of growth are not necessarily closely connected together, for plants may differ much in their seeds and little when full-grown, and conversely may yield seeds hardly distinguishable, yet differ much when full-grown. In the several breeds of poultry, descended from a single species, differences in the eggs and chickens, in the plumage at the first and subsequent moults, in the comb and wattles during maturity, are all inherited. With man peculiarities in the milk and second teeth, of which I have received the details, are inheritable, and with man longevity is often transmitted. So again with our improved breeds of cattle and sheep, early maturity, including the early development of the teeth, and with certain breeds of fowl the early appearance of secondary sexual characters, all come under the same head of inheritance at corresponding periods. {76}

Numerous analogous facts could be given. The silk-moth, perhaps, offers the best instance; for in the breeds which transmit their characters truly, the eggs differ in size, colour, and shape;—the caterpillars differ, in moulting three or four times, in colour, even in having a dark-coloured mark like an eyebrow, and in the loss of certain instincts;—the cocoons differ in size, shape, and in the colour and quality of the silk; these several differences being followed by slight or barely distinguishable differences in the mature moth.

But it may be said that, if in the above cases a new peculiarity is inherited, it must be at the corresponding stage of development; for an egg or seed can resemble only an egg or seed, and the horn in a full-grown ox can resemble only a horn. The following cases show inheritance at corresponding periods more plainly, because they refer to peculiarities which might have supervened, as far as we can see, earlier or later in life, yet are inherited at the same period at which they first appeared.

In the Lambert family the porcupine-like excrescences appeared in the father and sons at the same age, namely, about nine weeks after birth.[164] In the extraordinary hairy family described by Mr. Crawfurd,[165] children were produced during three generations with hairy ears; in the father the hair began to grow over his body at six years old; in his daughter somewhat earlier, namely, at one year; and in both generations the milk teeth appeared late in life, the permanent teeth being afterwards singularly deficient. Greyness of hair at an unusually early age has been transmitted in some families. These cases border on diseases inherited at corresponding periods of life, to which I shall immediately refer. {77}

It is a well-known peculiarity with almond-tumbler pigeons, that the full beauty and peculiar character of the plumage does not appear until the bird has moulted two or three times. Neumeister describes and figures a breed of pigeons in which the whole body is white except the breast, neck, and head; but before the first moult all the white feathers acquire coloured edges. Another breed is more remarkable: its first plumage

is black, with rusty-red wing-bars and a crescent-shaped mark on the breast; these marks then became white, and remain so during three or four moults; but after this period the white spreads over the body, and the bird loses its beauty.[166] Prize canary-birds have their wings and tail black: "this colour, however, is only retained until the first moult, so that they must be exhibited ere the change takes place. Once moulted, the peculiarity has ceased. Of course all the birds emanating from this stock have black wings and tails the first year."[167] A curious and somewhat analogous account has been given[168] of a family of wild pied rooks which were first observed in 1798, near Chalfont, and which every year from that date up to the period of the published notice, viz. 1837, "have several of their brood particoloured, black and white. This variegation of the plumage, however, disappears with the first moult; but among the next young families there are always a few pied ones." These changes of plumage, which appear and are inherited at various corresponding periods of life in the pigeon, canary-bird, and rook, are remarkable, because the parent-species undergo no such change.

Inherited diseases afford evidence in some respects of less value than the foregoing cases, because diseases are not necessarily connected with any change in structure; but in other respects of more value, because the periods have been more carefully observed. Certain diseases are communicated to the child apparently by a process like inoculation, and the child is from the first affected; such cases may be here passed over. Large classes of diseases usually appear at certain ages, such as St. Vitus's dance in youth, consumption in early mid-life, gout later, and apoplexy still later; and these are naturally inherited at the same period. But even in diseases of this class, instances have been recorded, as with St. Vitus's dance, showing that an unusually early or late {78} tendency to the disease is inheritable.[169] In most cases the appearance of any inherited disease is largely determined by certain critical periods in each person's life, as well as by unfavourable conditions. There are many other diseases, which are not attached to any particular period, but which certainly tend to appear in the child at about the same age at which the parent was first attacked. An array of high authorities, ancient and modern, could be given in support of this proposition. The illustrious Hunter believed in it; and Piorry[170] cautions the physician to look closely to the child at the period when any grave inheritable disease attacked the parent. Dr. Prosper Lucas,[171] after collecting facts from every source, asserts that affections of all kinds, though not related to any particular period of life, tend to reappear in the offspring at whatever period of life they first appeared in the progenitor.

As the subject is important, it may be well to give a few instances, simply as illustrations, not as proof; for proof, recourse must be had to the authorities above quoted. Some of the following cases have been selected for the sake of showing that, when a slight departure from the rule occurs, the child is affected somewhat earlier in life than the parent. In the family of Le Compte blindness was inherited during three generations, and no less than thirty-seven children and grandchildren were all affected at about the same age, namely seventeen or eighteen.[172] In another case a father and his four children all became blind at twenty-one years old; in another, a grandmother grew blind at thirty-five, her daughter at nineteen, and three grandchildren at the ages of thirteen and eleven.[173] So with deafness, two brothers, their father and paternal grandfather, all became deaf at the age of forty.[174]

Esquirol gives several striking instances of insanity coming on at the same age, as that of a grandfather, father, and son, who all committed suicide near their fiftieth year. Many other cases could be given, as of a whole family who became insane at the age of forty.[175] Other cerebral affections sometimes follow the same rule,—for instance,

epilepsy and apoplexy. A woman died of the latter disease when sixty-three years old; one of her daughters at forty-three, and the other at sixty-seven: the latter had twelve children, who all died from tubercular meningitis.[176] I mention this latter case because it illustrates a frequent occurrence, namely, a change in the precise nature of an inherited disease, though still affecting the same organ.

Asthma has attacked several members of the same family when forty years old, and other families during infancy. The most different diseases, as angina pectoris, stone in the bladder, and various affections of the skin, have appeared in successive generations at nearly the same age. The little finger of a man began from some unknown cause to grow inwards, and the same finger in his two sons began at the same age to bend inwards in a similar manner. Strange and inexplicable neuralgic affections have caused parents and children to suffer agonies at about the same period of life.[177] {79}

I will give only two other cases, which are interesting as illustrating the disappearance as well as the appearance of disease at the same age. Two brothers, their father, their paternal uncles, seven cousins, and their paternal grandfather, were all similarly affected by a skin-disease, called pityriasis versicolor; "the disease, strictly limited to the males of the family (though transmitted through the females), usually appeared at puberty, and disappeared at about the age of forty or forty-five years." The second case is that of four brothers, who when about twelve years old suffered almost every week from severe headaches, which were relieved only by a recumbent position in a dark room. Their father, paternal uncles, paternal grandfather, and paternal granduncles all suffered in the same way from headaches, which ceased at the age of fifty-four or fifty-five in all those who lived so long. None of the females of the family were affected.[178]

It is impossible to read the foregoing accounts, and the many others which have been recorded, of diseases coming on during three or even more generations, at the same age in several members of the same family, especially in the case of rare affections in which the coincidence cannot be attributed to chance, and doubt that there is a strong tendency to inheritance in disease at corresponding periods of life. When the rule fails, the disease is apt to come on earlier in the child than in the parent; the exceptions in the other direction being vey much rarer. Dr. Lucas[179] alludes to several cases of inherited diseases coming on at an earlier period. I have already given one striking instance with blindness during three generations; and Mr. Bowman remarks that this frequently occurs with cataract. With cancer there seems to be a peculiar liability to earlier inheritance: Mr. Paget, who has particularly attended to this subject, and tabulated a large number of cases, informs me that he believes {80} that in nine cases out of ten the later generation suffers from the disease at an earlier period than the previous generation. He adds, "In the instances in which the opposite relation holds, and the members of later generations have cancer at a later age than their predecessors, I think it will be found that the non-cancerous parents have lived to extreme old ages." So that the longevity of a non-affected parent seems to have the power of determining in the offspring the fatal period; and we thus apparently get another element of complexity in inheritance.

The facts, showing that with certain diseases the period of inheritance occasionally or even frequently advances, are important with respect to the general descent-theory, for they render it in some degree probable that the same thing would occur with ordinary modifications of structure. The final result of a long series of such advances would be the gradual obliteration of characters proper to the embryo and larva, which would thus come to resemble more and more closely the mature parent-form. But any structure which was of service to the embryo or larva would be preserved by the destruction at this stage of growth

of each individual which manifested any tendency to lose at too early an age its own proper character.

Finally, from the numerous races of cultivated plants and domestic animals, in which the seed or eggs, the young or old, differ from each other and from their parent-species;—from the cases in which new characters have appeared at a particular period, and afterwards have been inherited at the same period;—and from what we know with respect to disease, we must believe in the truth of the great principle of inheritance at corresponding periods of life.

Summary of the three preceding Chapters.—Strong as is the force of inheritance, it allows the incessant appearance of new characters. These, whether beneficial or injurious, of the most trifling importance, such as a shade of colour in a flower, a coloured lock of hair, or a mere gesture; or of the highest importance, as when affecting the brain or an organ so perfect and complex as the eye; or of so grave a nature as to deserve to be called a {81} monstrosity, or so peculiar as not to occur normally in any member of the same natural class, are all sometimes strongly inherited by man, the lower animals, and plants. In numberless cases it suffices for the inheritance of a peculiarity that one parent alone should be thus characterised. Inequalities in the two sides of the body, though opposed to the law of symmetry, may be transmitted. There is a considerable body of evidence showing that even mutilations, and the effects of accidents, especially or perhaps exclusively when followed by disease, are occasionally inherited. There can be no doubt that the evil effects of long-continued exposure in the parent to injurious conditions are sometimes transmitted to the offspring. So it is, as we shall see in a future chapter, with the effects of the use and disuse of parts, and of mental habits. Periodical habits are likewise transmitted, but generally, as it would appear, with little force.

Hence we are led to look at inheritance as the rule, and non-inheritance as the anomaly. But this power often appears to us in our ignorance to act capriciously, transmitting a character with inexplicable strength or feebleness. The very same peculiarity, as the weeping habit of trees, silky-feathers, &c., may be inherited either firmly or not at all by different members of the same group, and even by different individuals of the same species, though treated in the same manner. In this latter case we see that the power of transmission is a quality which is merely individual in its attachment. As with single characters, so it is with the several concurrent slight differences which distinguish sub-varieties or races; for of these, some can be propagated almost as truly as species, whilst others cannot be relied on. The same rule holds good with plants, when propagated by bulbs, offsets, &c., which in one sense still form parts of the same individual, for some varieties retain or inherit through successive bud-generations their character far more truly than others.

Some characters not proper to the parent-species have certainly been inherited from an extremely remote epoch, and may therefore be considered as firmly fixed. But it is doubtful whether length of inheritance in itself gives fixedness of character; though the chances are {82} obviously in favour of any character which has long been transmitted true or unaltered, still being transmitted true as long as the conditions of life remain the same. We know that many species, after having retained the same character for countless ages, whilst living under their natural conditions, when domesticated have varied in the most diversified manner, that is, have failed to transmit their original form; so that no character appears to be absolutely fixed. We can sometimes account for the failure of inheritance by the conditions of life being opposed to the development of certain characters; and still oftener, as with plants cultivated by grafts and buds, by the conditions causing new and slight modifications incessantly to appear. In this latter case it is not that inheritance wholly fails, but that new characters are continually superadded. In some few cases, in which both parents are similarly characterised, inheritance seems to gain so much force by the combined action of the two parents, that it counteracts its own power, and a new modification is the result.

In many cases the failure of the parents to transmit their likeness is due to the breed having been at some former period crossed; and the child takes after his grandparent or more remote ancestor of foreign blood. In other cases, in which the breed has not been crossed, but some ancient character has been lost through variation, it occasionally reappears through reversion, so that the parents apparently fail to transmit their own likeness. In all cases, however, we may safely conclude that the child inherits all its characters from its parents, in whom certain characters are latent, like the secondary sexual characters of one sex in the other. When, after a long succession of bud-generations, a flower or fruit becomes separated into distinct segments, having the colours or other attributes of both parent-forms, we cannot doubt that these characters were latent in the earlier buds, though they could not then be detected, or could be detected only in an intimately commingled state. So it is with animals of crossed parentage, which with advancing years occasionally exhibit characters derived from one of their two parents, of which not a trace could at first be perceived. Certain monstrosities, which resemble what naturalists call the typical form of the group in question, apparently come under the same law of reversion. It is assuredly an astonishing {83}
fact that the male and female sexual elements, that buds, and even full-grown animals, should retain characters, during several generations in the case of crossed breeds, and during thousands of generations in the case of pure breeds, written as it were in invisible ink, yet ready at any time to be evolved under the requisite conditions.

What these conditions are, we do not in many cases at all know. But the act of crossing in itself, apparently from causing some disturbance in the organisation, certainly gives a strong tendency to the reappearance of long-lost characters, both corporeal and mental, independently of those derived from the cross. A return of any species to its natural conditions of life, as with feral animals and plants, favours reversion; though it is certain that this tendency exists, we do not know how far it prevails, and it has been much exaggerated. On the other hand, the crossed offspring of plants which have had their organisation disturbed by cultivation, are more liable to reversion than the crossed offspring of species which have always lived under their natural conditions.

When distinguishable individuals of the same family, or races, or species are crossed, we see that the one is often prepotent over the other in transmitting its own character. A race may possess a strong power of inheritance, and yet when crossed, as we have seen with trumpeter-pigeons, yield to the prepotency of every other race. Prepotentcy of transmission may be equal in the two sexes of the same species, but often runs more strongly in one sex. It plays an important part in determining the rate at which one race can be modified or wholly absorbed by repeated crosses with another. We can seldom tell what makes one race or species prepotent over another; but it sometimes depends on the same character being present and visible in one parent, and latent or potentially present in the other.

Characters may first appear in either sex, but oftener in the male than in the female, and afterwards be transmitted to the offspring of the same sex. In this case we may feel confident that the peculiarity in question is really present though latent in the opposite sex; hence the father may transmit through his daughter any character to his grandson; and the mother conversely to her granddaughter. We thus learn, and the fact is an important one, {84}
that transmission and development are distinct powers. Occasionally these two powers seem to be antagonistic, or incapable of combination in the same individual; for several cases have been recorded in which the son has not directly inherited a character from his father, or directly transmitted it to his son, but has received it by transmission through his non-affected mother, and transmitted it through his non-affected daughter. Owing to inheritance being limited by sex, we can see how secondary sexual characters may first have arisen under nature; their preservation and accumulation being dependent on their service to either sex.

At whatever period of life a new character first appears, it generally remains latent in the offspring until a corresponding age is attained, and then it is developed. When this rule fails, the child generally exhibits the character at an earlier period than the parent. On this principle of inheritance at corresponding periods, we can understand how it is that most animals display from the germ to maturity such a marvellous succession of characters.

Finally, though much remains obscure with respect to Inheritance, we may look at the following laws as fairly well established. Firstly, a tendency in every character, new and old, to be transmitted by seminal and bud generation, though often counteracted by various known and unknown causes. Secondly, reversion or atavism, which depends on transmission and development being distinct powers: it acts in various degrees and manners through both seminal and bud generation. Thirdly, prepotency of transmission, which may be confined to one sex, or be common to both sexes of the prepotent form. Fourthly, transmission, limited by sex, generally to the same sex in which the inherited character first appeared. Fifthly, inheritance at corresponding periods of life, with some tendency to the earlier development of the inherited character. In these laws of Inheritance, as displayed under domestication, we see an ample provision for the production, through variability and natural selection, of new specific forms.

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CHAPTER XV.

ON CROSSING.

FREE INTERCROSSING OBLITERATES THE DIFFERENCES BETWEEN ALLIED BREEDS—WHEN THE NUMBERS OF TWO COMMINGLING BREEDS ARE UNEQUAL, ONE ABSORBS THE OTHER—THE RATE OF ABSORPTION DETERMINED BY PREPOTENCY OF TRANSMISSION, BY THE CONDITIONS OF LIFE, AND BY NATURAL SELECTION—ALL ORGANIC BEINGS OCCASIONALLY INTERCROSS; APPARENT EXCEPTIONS—ON CERTAIN CHARACTERS INCAPABLE OF FUSION; CHIEFLY OR EXCLUSIVELY THOSE WHICH HAVE SUDDENLY APPEARED IN THE INDIVIDUAL—ON THE MODIFICATION OF OLD RACES, AND THE FORMATION OF NEW RACES, BY CROSSING—SOME CROSSED RACES HAVE BRED TRUE FROM THEIR FIRST PRODUCTION—ON THE CROSSING OF DISTINCT SPECIES IN RELATION TO THE FORMATION OF DOMESTIC RACES.

In the two previous chapters, when discussing reversion and prepotency, I was necessarily led to give many facts on crossing. In the present chapter I shall consider the part which crossing plays in two opposed directions,—firstly, in obliterating characters, and consequently in preventing the formation of new races; and secondly, in the modification of old races, or in the formation of new and intermediate races, by a combination of characters. I shall also show that certain characters are incapable of fusion.

The effects of free or uncontrolled breeding between the members of the same variety or of closely allied varieties are important; but are so obvious that they need not be discussed at much length. It is free intercrossing which chiefly gives uniformity, both under nature and under domestication, to the individuals of the same species or variety, when they live mingled together and are not exposed to any cause inducing excessive variability. The prevention of free crossing, and the intentional matching of individual animals, are the corner-stones of the breeder's art. No man in his senses would expect to improve or modify a breed in any particular manner, or keep an old breed true and distinct, unless he separated his animals. The killing of inferior animals in each generation comes to the same thing as {86} their separation. In savage and semi-civilised countries, where the inhabitants have not the means of separating their animals, more than a single breed of the same species rarely or never exists. In former times, even in a country so civilised as North America, there were no distinct races of sheep, for all had been mingled together.[180] The celebrated agriculturist

Marshall[181] remarks that "sheep that are kept within fences, as well as shepherded flocks in open countries, have generally a similarity, if not a uniformity, of character in the individuals of each flock;" for they breed freely together, and are prevented from crossing with other kinds; whereas in the unenclosed parts of England the unshepherded sheep, even of the same flock, are far from true or uniform, owing to various breeds having mingled and crossed. We have seen that the half-wild cattle in the several British parks are uniform in character in each; but in the different parks, from not having mingled and crossed during many generations, they differ in a slight degree.

We cannot doubt that the extraordinary number of varieties and sub-varieties of the pigeon, amounting to at least one hundred and fifty, is partly due to their remaining, differently from other domesticated birds, paired for life when once matched. On the other hand, breeds of cats imported into this country soon disappear, for their nocturnal and rambling habits render it hardly possible to prevent free crossing. Rengger[182] gives an interesting case with respect to the cat in Paraguay: in all the distant parts of the kingdom it has assumed, apparently from the effects of the climate, a peculiar character, but near the capital this change has been prevented, owing, as he asserts, to the native animal frequently crossing with cats imported from Europe. In all cases like the foregoing, the effects of an occasional cross will be augmented by the increased vigour and fertility of the crossed offspring, of which fact evidence will hereafter be given; for this will lead to the mongrels increasing more rapidly than the pure parent-breeds.

When distinct breeds are allowed to cross freely, the result will be a heterogenous body; for {87}
instance, the dogs in Paraguay are far from uniform, and can no longer be affiliated to their parent-races.[183] The character which a crossed body of animals will ultimately assume must depend on several contingencies,—namely, on the relative numbers of the individuals belonging to the two or more races which are allowed to mingle; on the prepotency of one race over the other in the transmission of character; and on the conditions of life to which they are exposed. When two commingled breeds exist at first in nearly equal numbers, the whole will sooner or later become intimately blended, but not so soon, both breeds being equally favoured in all respects, as might have been expected. The following calculation[184] shows that this is the case: if a colony with an equal number of black and white men were founded, and we assume that they marry indiscriminately, are equally prolific, and that one in thirty annually dies and is born; then "in 65 years the number of blacks, whites, and mulattoes would be equal. In 91 years the whites would be 1-10th, the blacks 1-10th, and the mulattoes, or people of intermediate degrees of colour, 8-10ths of the whole number. In three centuries not 1-100th part of the whites would exist."

When one of two mingled races exceeds the other greatly in number, the latter will soon be wholly, or almost wholly, absorbed and lost.[185] Thus European pigs and dogs have been largely introduced into the islands of the Pacific Ocean, and the native races have been absorbed and lost in the course of about fifty or sixty years;[186] but the imported races no doubt were favoured. Rats may be considered as semi-domesticated animals. Some snake-rats (*Mus alexandrinus*) escaped in the Zoological Gardens of London, "and for a long time afterwards the keepers frequently caught cross-bred rats, at first half-breds, afterwards with less and less of the character of the snake-rat, till at length all traces of it disappeared."[187]
On the other hand, in some parts of London, especially near the docks, where fresh rats are {88}
frequently imported, an endless variety of intermediate forms may be found between the brown, black, and snake rat, which are all three usually ranked as distinct species.

How many generations are necessary for one species or race to absorb another by repeated crosses has often been discussed;[188] and the requisite number has probably been much exaggerated. Some writers have maintained that a dozen, or score, or even more generations, are necessary; but this in itself is improbable, for in the tenth generation there

will be only 1-1024th part of foreign blood in the offspring. Gärtner found,[189] that with plants one species could be made to absorb another in from three to five generations, and he believes that this could always be effected in from six to seventh generations. In one instance, however, Kölreuter[190] speaks of the offspring of *Mirabilis vulgaris*, crossed during eight successive generations by *M. longiflora*, as resembling this latter species so closely, that the most scrupulous observer could detect "vix aliquam notabilem differentiam;"—he succeeded, as he says, "ad plenariam fere transmutationem." But this expression shows that the act of absorption was not even then absolutely complete, though these crossed plants contained only the 1-256th part of *M. vulgaris*. The conclusions of such accurate observers as Gärtner and Kölreuter are of far higher worth than those made without scientific aim by breeders. The most remarkable statement which I have met with of the persistent endurance of the effects of a single cross is given by Fleischmann,[191] who, in reference to German sheep, says "that the original coarse sheep have 5500 fibres of wool on a square inch; grades of the third or fourth Merino cross produced about 8000, the twentieth cross 27,000, the perfect pure Merino blood 40,000 to 48,000." So that in this case common German sheep crossed twenty times successively with Merinos have not by any means acquired wool as fine as that of the pure breed. In all cases, the rate of absorption will depend largely on the conditions of life being favourable to any particular character; and we {89}
may suspect that there would be under the climate of Germany a constant tendency to degeneration in the wool of Merinos, unless prevented by careful selection; and thus perhaps the foregoing remarkable case may be explained. The rate of absorption must also depend on the amount of distinguishable difference between the two forms which are crossed, and especially, as Gärtner insists, on prepotency of transmission in the one form over the other. We have seen in the last chapter that one of two French breeds of sheep yielded up its character, when crossed with Merinos, very much slower than the other; and the common German sheep referred to by Fleischmann may present an analogous case. But in all cases there will be during many subsequent generations more or less liability to reversion, and it is this fact which has probably led authors to maintain that a score or more of generations are requisite for one race to absorb another. In considering the final result of the commingling of two or more breeds, we must not forget that the act of crossing in itself tends to bring back long-lost characters not proper to the immediate parent-forms.

With respect to the influence of the conditions of life on any two breeds which are allowed to cross freely, unless both are indigenous and have long been accustomed to the country where they live, they will, in all probability, be unequally affected by the conditions, and this will modify the result. Even with indigenous breeds, it will rarely or never occur that both are equally well adapted to the surrounding circumstances; more especially when permitted to roam freely, and not carefully tended, as will generally be the case with breeds allowed to cross. As a consequence of this, natural selection will to a certain extent come into action, and the best fitted will survive, and this will aid in determining the ultimate character of the commingled body.

How long a time it would require before such a crossed body of animals would assume within a limited area a uniform character no one can say; that they would ultimately become uniform from free intercrossing, and from the survival of the fittest, we may feel assured; but the character thus acquired would rarely or never, as we may infer from the several previous considerations, be exactly intermediate between that of the two parent-breeds. {90}
With respect to the very slight differences by which the individuals of the same sub-variety, or even of allied varieties, are characterised, it is obvious that free crossing would soon obliterate such small distinctions. The formation of new varieties, independently of selection, would also thus be prevented; except when the same variation continually recurred from the action of some strongly predisposing cause. Hence we may conclude that free crossing has in all cases played an important part in giving to all the members of the

same domestic race, and of the same natural species, uniformity of character, though largely modified by natural selection and by the direct action of the surrounding conditions.

On the possibility of all organic beings occasionally intercrossing.—But it may be asked, can free crossing occur with hermaphrodite animals and plants? All the higher animals, and the few insects which have been domesticated, have separated sexes, and must inevitably unite for each birth. With respect to the crossing of hermaphrodites, the subject is too large for the present volume, and will be more properly treated in a succeeding work. In my 'Origin of Species,' however, I have given a short abstract of the reasons which induce me to believe that all organic beings occasionally cross, though perhaps in some cases only at long intervals of time.[192] I will here just recall the fact that many plants, though hermaphrodite in structure, are unisexual in function;—such as those called by C. K. Sprengel *dichogamous*, in which the pollen and stigma of the same flower are matured at different periods; or those called by me *reciprocally dimorphic*, in which the flower's own pollen is not fitted to fertilise its own stigma; or again, the many kinds in which curious mechanical contrivances exist, effectually preventing self-fertilisation. There are, however, many hermaphrodite plants which are not in any way specially constructed to favour intercrossing, but which nevertheless commingle almost as freely as animals with separated sexes. This is the case with cabbages, radishes, and onions, as I know from having {91} experimented on them: even the peasants of Liguria say that cabbages must be prevented "from falling in love" with each other. In the orange tribe, Gallesio[193] remarks that the amelioration of the various kinds is checked by their continual and almost regular crossing. So it is with numerous other plants.

Nevertheless some cultivated plants can be named which rarely intercross, as the common pea, or which never intercross, as I have reason to believe is the case with the sweet-pea (*Lathyrus odoratus*); yet the structure of these flowers certainly favours an occasional cross. The varieties of the tomato and aubergine (*Solanum*) and pimenta (*Pimenta vulgaris?*) are said[194] never to cross, even when growing alongside each other. But it should be observed that these are all exotic plants, and we do not know how they would behave in their native country when visited by the proper insects.

It must also be admitted that some few natural species appear under our present state of knowledge to be perpetually self-fertilised, as in the case of the Bee Ophrys (*O. apifera*), though adapted in its structure to be occasionally crossed. The *Leersia oryzoides* produces minute enclosed flowers which cannot possibly be crossed, and these alone, to the exclusion of the ordinary flowers, have as yet been known to yield seed.[195] A few additional and analogous cases could be advanced. But these facts do not make me doubt that it is a general law of nature that the individuals of the same species occasionally intercross, and that some great advantage is derived from this act. It is well known (and I shall hereafter have to give instances) that some plants, both indigenous and naturalised, rarely or never produce flowers; or, if they flower, never produce seeds. But no one is thus led to doubt that it is a general law of nature that phanerogamic plants should produce flowers, and that these flowers should produce seed. When they fail, we believe that such plants would perform their proper functions under different conditions, or that they formerly did so and will do so again. On analogous grounds, I believe that the few flowers which do not now intercross, {92} either would do so under different conditions, or that they formerly fertilised each other at intervals—the means for effecting this being generally still retained—and they will do so again at some future period, unless indeed they become extinct. On this view alone, many points in the structure and action of the reproductive organs in hermaphrodite plants and animals are intelligible,—for instance, the male and female organs never being so completely enclosed as to render access from without impossible. Hence we may conclude that the most important of all the means for giving uniformity to the individuals of the same

species, namely, the capacity of occasionally intercrossing, is present, or has been formerly present, with all organic beings.

On certain Characters not blending.—When two breeds are crossed their characters usually become intimately fused together; but some characters refuse to blend, and are transmitted in an unmodified state either from both parents or from one. When grey and white mice are paired, the young are not piebald nor of an intermediate tint, but are pure white or of the ordinary grey colour: so it is when white and common collared turtle-doves are paired. In breeding Game fowls, a great authority, Mr. J. Douglas, remarks, "I may here state a strange fact: if you cross a black with a white game, you get birds of both breeds of the clearest colour." Sir R. Heron crossed during many years white, black, brown, and fawn-coloured Angora rabbits, and never once got these colours mingled in the same animal, but often all four colours in the same litter.[196] Additional cases could be given, but this form of inheritance is very far from universal even with respect to the most distinct colours. 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 take after either parent. 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 {93} or are quite destitute of them. According to Rengger, the hairless condition of the Paraguay dog is either perfectly or not at all transmitted to its mongrel offspring; but I have seen one partial exception in a dog of this parentage which had part of its skin hairy, and part naked; the parts being distinctly separated as in a piebald animal. 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. Some crossed pigs raised by Sir R. Heron between the solid-hoofed and common pig had not all four feet in an intermediate condition, but two feet were furnished with properly divided, and two with united hoofs.

Analogous facts have been observed with plants: Major Trevor Clarke crossed the little, glabrous-leaved, annual stock (*Matthiola*), with pollen of a large, red-flowered, rough-leaved, biennial stock, called *cocardeau* by the French, and the result was that half the seedlings had glabrous and the other half rough leaves, but none had leaves in an intermediate state. That the glabrous seedlings were the product of the rough-leaved variety, and not accidentally of the mother-plant's own pollen, was shown by their tall and strong habit of growth.[197] In the succeeding generations raised from the rough-leaved crossed seedlings, some glabrous plants appeared, showing that the glabrous character, though incapable of blending with and modifying the rough leaves, was all the time latent in this family of plants. The numerous plants formerly referred to, which I raised from reciprocal crosses between the peloric and common Antirrhinum, offer a nearly parallel case; for in the first generation all the plants resembled the common form, and in the next generation, out of one hundred and thirty-seven plants, two alone were in an intermediate condition, the others perfectly resembling either the peloric or common form. Major Trevor Clarke also fertilised the above-mentioned red-flowered stock with pollen from the purple Queen stock, and about half the seedlings scarcely differed in habit, and not at all in the red colour of the flower, from the mother-plant, the other half bearing blossoms of a rich purple, closely like those of the paternal plant. Gärtner crossed many white and yellow-flowered species and varieties of Verbascum; and these colours were never blended, but the offspring bore either pure white or pure yellow blossoms; the former in the larger proportion.[198] Dr. Herbert raised many seedlings, as he informed me, from Swedish turnips crossed by two other varieties, and these never produced flowers of an intermediate tint, but always like one of their parents. I fertilised the purple sweet-pea (*Lathyrus odoratus*), which has a dark reddish-purple standard-petal and violet-

coloured wings and keel, with pollen of the painted-lady sweet-pea, which has a pale cherry-coloured standard, and almost white wings and keel; and from the same pod I twice raised plants perfectly resembling both sorts; the greater number resembling the father. So perfect was the resemblance, that I should have thought there had been some mistake, if the plants which were at first identical with the paternal variety, namely, the painted-lady, had not later in the season produced, as mentioned in a former chapter, flowers blotched and streaked with dark purple. I raised grandchildren and great-grandchildren from these crossed plants, and they continued to resemble the painted-lady, but during the later generations became rather more blotched with purple, yet none reverted completely to the original mother-plant, the purple sweet-pea. The following case is slightly different, but still shows the same principle: Naudin[199] raised numerous hybrids between the yellow *Linaria vulgaris* and the purple *L. purpurea*, and during three successive generations the colours kept distinct in different parts of the same flower. {94}

From such cases as the foregoing, in which the offspring of the first generation perfectly resemble either parent, we come by a small step to those cases in which differently coloured flowers borne on the same root resemble both parents, and by another step to those in which the same flower or fruit is striped or blotched with the two parental colours, or bears a single stripe of the colour or other characteristic quality of one of the parent-forms. With hybrids and mongrels it frequently or even generally happens that one part of the body resembles more or less closely one parent and another part the other parent; and here again some resistance to fusion, or, what comes to the same thing, some mutual affinity between the organic atoms of the same nature, apparently comes into play, for otherwise all parts of the body would be equally intermediate in character. So again, when the offspring of hybrids or mongrels, which are themselves nearly intermediate in character, revert either wholly or by segments to their ancestors, the principle of the affinity of similar, or the repulsion of dissimilar atoms, must come into action. To this principle, which seems to be extremely general, we shall recur in the chapter on pangenesis.

It is remarkable, as has been strongly insisted upon by Isidore Geoffroy St. Hilaire in regard to animals, that the transmission of characters without fusion occurs most rarely when species are crossed; I know of one exception alone, namely, with the hybrids naturally produced between the common and hooded crow (*Corvus corone* and *cornix*), which, however, are closely allied species, differing in nothing except colour. Nor have I met with any well-ascertained cases of transmission of this kind, even when one form is strongly prepotent over another, when two races are crossed which have been slowly formed by man's selection, and therefore resemble to a certain extent natural species. Such cases as puppies in the same litter closely resembling two distinct breeds, are probably due to super-fœtation,—that is, to the influence of two fathers. All the characters above enumerated, which are transmitted in a perfect state to some of the offspring and not to others,—such as distinct colours, nakedness of skin, smoothness of leaves, absence of horns or tail, additional toes, pelorism, dwarfed structure, &c.,—have all been known to appear suddenly in individual animals and plants. From this fact, and from the several slight, aggregated differences which distinguish domestic races and species from each other, not being liable to this peculiar form of transmission, we may conclude that it is in some way connected with the sudden appearance of the characters in question. {95}

On the Modification of old Races and the Formation of new Races by Crossing.—We have hitherto chiefly considered the effects of crossing in giving uniformity of character; we must now look to an opposite result. There can be no doubt that crossing, with the aid of rigorous selection during several generations, has been a potent means in modifying old races, and in forming new ones. Lord Orford crossed his famous stud of greyhounds once with the

bulldog, which breed was chosen from being deficient in scenting powers, and from having what was wanted, courage and perseverance. In the course of six or seven generations all traces of the external form of the bulldog were eliminated, but courage and perseverance remained. Certain pointers have been crossed, as I hear from the Rev. W. D. Fox, with the foxhound, to give them dash and speed. Certain strains of Dorking fowls have had a slight infusion of Game blood; and I have known a great fancier who on a single occasion crossed his turbit-pigeons with barbs, for the sake of gaining greater breadth of beak.

In the foregoing cases breeds have been crossed once, for the sake of modifying some particular character; but with most of the improved races of the pig, which now breed true, there have been repeated crosses,—for instance, the improved Essex owes its excellence to repeated crosses with the Neapolitan, together probably with some infusion of Chinese blood.[200] So with our British sheep: almost all the races, except the Southdown, have been largely crossed; "this, in fact, has been the history of our principal breeds."[201] To give an example, the "Oxfordshire Downs" now rank as an established breed.[202] They were produced about the year 1830 by crossing "Hampshire and in some instances Southdown ewes with Cotswold rams:" now the Hampshire ram was itself produced by repeated crosses between the native Hampshire sheep and Southdowns; and the long-woolled Cotswold were {96}
improved by crosses with the Leicester, which latter again is believed to have been a cross between several long-woolled sheep. Mr. Spooner, after considering the various cases which have been carefully recorded, concludes "that from a judicious pairing of cross-bred animals it is practicable to establish a new breed." On the Continent the history of several crossed races of cattle and of other animals has been well ascertained. To give one instance: the King of Wurtemberg, after twenty-five years' careful breeding, that is after six or seven generations, made a new breed of cattle from a cross between a Dutch and Swiss breed, combined with other breeds.[203] The Sebright bantam, which breeds as true as any other kind of fowl, was formed about sixty years ago by a complicated cross.[204] Dark Brahmas, which are believed by some fanciers to constitute a distinct species, were undoubtedly formed[205] in the United States, within a recent period, by a cross between Chittagongs and Cochins. With plants I believe there is little doubt that some kinds of turnips, now extensively cultivated, are crossed races; and the history of a variety of wheat which was raised from two very distinct varieties, and which after six years' culture presented an even sample, has been recorded on good authority.[206]

Until quite lately, cautious and experienced breeders, though not averse to a single infusion of foreign blood, were almost universally convinced that the attempt to establish a new race, intermediate between two widely distinct races, was hopeless: "they clung with superstitious tenacity to the doctrine of purity of blood, believing it to be the ark in which alone true safety could be found."[207] Nor was this conviction unreasonable: when two distinct races are crossed, the offspring of the first generation are generally nearly uniform in character; but even this sometimes fails to be the case, especially with crossed dogs and fowls, the young of which from the first are sometimes much diversified. As cross-bred {97}
animals are generally of large size and vigorous, they have been raised in great numbers for immediate consumption. But for breeding they are found to be utterly useless; for though they may be themselves uniform in character, when paired together they yield during many generations offspring astonishingly diversified. The breeder is driven to despair, and concludes that he will never form an intermediate race. But from the cases already given, and from others which have been recorded, it appears that patience alone is necessary; as Mr. Spooner remarks, "nature opposes no barrier to successful admixture; in the course of time, by the aid of selection and careful weeding, it is practicable to establish a new breed." After six or seven generations the hoped-for result will in most cases be obtained; but even then an occasional reversion, or failure to keep true, may be expected. The attempt,

however, will assuredly fail if the conditions of life be decidedly unfavourable to the characters of either parent-breed.[208]

Although the grandchildren and succeeding generations of cross-bred animals are generally variable in an extreme degree, some curious exceptions to the rule have been observed, both with crossed races and species. Thus Boitard and Corbié[209] assert that from a Pouter and a Runt "a Cavalier will appear, which we have classed amongst pigeons of pure race, because it transmits all its qualities to its posterity." The editor of the 'Poultry Chronicle'[210] bred some bluish fowls from a black Spanish cock and a Malay hen; and these remained true to colour "generation after generation." The Himalayan breed of rabbits was certainly formed by crossing two sub-varieties of the silver-grey rabbit; although it suddenly assumed its present character, which differs much from that of either parent-breed, yet it has ever since been easily and truly propagated. I crossed some Labrador and Penguin ducks, and recrossed the mongrels with Penguins; afterwards, most of the ducks reared during three generations were nearly uniform in character, being brown with a white crescentic mark on the lower part of the breast, and with some white spots at the base of the beak; so that by the {98} aid of a little selection a new breed might easily have been formed. In regard to crossed varieties of plants, Mr. Beaton remarks[211] that "Melville's extraordinary cross between the Scotch kale and an early cabbage is as true and genuine as any on record;" but in this case no doubt selection was practised. Gärtner[212] has given five cases of hybrids, in which the progeny kept constant; and hybrids between *Dianthus armeria* and *deltoides* remained true and uniform to the tenth generation. Dr. Herbert likewise showed me a hybrid from two species of Loasa which from its first production had kept constant during several generations.

We have seen in the earlier chapters, that some of our domesticated animals, such as dogs, cattle, pigs, &c., are almost certainly descended from more than one species, or wild race, if any one prefers to apply this latter term to forms which were enabled to keep distinct in a state of nature. Hence the crossing of aboriginally distinct species probably came into play at an early period in the formation of our present races. From Rütimeyer's observations there can be little doubt that this occurred with cattle; but in most cases some one of the forms which were allowed to cross freely, will, it is probable, have absorbed and obliterated the others. For it is not likely that semi-civilized men would have taken the necessary pains to modify by selection their commingled, crossed, and fluctuating stock. Nevertheless, those animals which were best adapted to their conditions of life would have survived through natural selection; and by this means crossing will often have indirectly aided in the formation of primeval domesticated breeds.

Within recent times, as far as animals are concerned, the crossing of distinct species has done little or nothing in the formation or modification of our races. It is not yet known whether the species of silk-moth which have been recently crossed in France will yield permanent races. In the fourth chapter I alluded with some hesitation to the statement that a new breed, between the hare and rabbit, called leporides, had been formed in France, and was found capable of propagating itself; but it is now positively affirmed[213] that this is an {99} error. With plants which can be multiplied by buds and cuttings, hybridisation has done wonders, as with many kinds of Roses, Rhododendrons, Pelargoniums, Calceolarias, and Petunias. Nearly all these plants can be propagated by seed; most of them freely; but extremely few or none come true by seed.

Some authors believe that crossing is the chief cause of variability,—that is, of the appearance of absolutely new characters. Some have gone so far as to look at it as the sole cause; but this conclusion is disproved by some of the facts given in the chapter on Bud-variation. The belief that characters not present in either parent or in their ancestors frequently originate from crossing is doubtful; that they occasionally thus arise is probable;

but this subject will be more conveniently discussed in a future chapter on the causes of Variability.

A condensed summary of this and of the three following chapters, together with some remarks on Hybridism, will be given in the nineteenth chapter.

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CHAPTER XVI.

CAUSES WHICH INTERFERE WITH THE FREE CROSSING OF VARIETIES—INFLUENCE OF DOMESTICATION ON FERTILITY.

DIFFICULTIES IN JUDGING OF THE FERTILITY OF VARIETIES WHEN CROSSED—VARIOUS CAUSES WHICH KEEP VARIETIES DISTINCT, AS THE PERIOD OF BREEDING AND SEXUAL PREFERENCE—VARIETIES OF WHEAT SAID TO BE STERILE WHEN CROSSED—VARIETIES OF MAIZE, VERBASCUM, HOLLYHOCK, GOURDS, MELONS, AND TOBACCO, RENDERED IN SOME DEGREE MUTUALLY STERILE—DOMESTICATION ELIMINATES THE TENDENCY TO STERILITY NATURAL TO SPECIES WHEN CROSSED—ON THE INCREASED FERTILITY OF UNCROSSED ANIMALS AND PLANTS FROM DOMESTICATION AND CULTIVATION.

The domesticated races of both animals and plants, when crossed, are with extremely few exceptions quite prolific,—in some cases even more so than the purely bred parent-races. The offspring, also, raised from such crosses are likewise, as we shall see in the following chapter, generally more vigorous and fertile than their parents. On the other hand, species when crossed, and their hybrid offspring, are almost invariability in some degree sterile; and here there seems to exist a broad and insuperable distinction between races and species. The importance of this subject as bearing on the origin of species is obvious; and we shall hereafter recur to it.

It is unfortunate how few precise observations have been made on the fertility of mongrel animals and plants during several successive generations. Dr. Broca[214] has remarked that no one has observed whether, for instance, mongrel dogs, bred *inter se*, are indefinitely fertile; yet, if a shade of infertility be detected by careful observation in the offspring of natural forms when crossed, it is thought that their specific distinction is proved. But so many breeds of sheep, cattle, pigs, dogs, and poultry, have been crossed and recrossed in various ways, that any sterility, if it had existed, would from being injurious almost {101} certainly have been observed. In investigating the fertility of crossed varieties many sources of doubt occur. Whenever the least trace of sterility between two plants, however closely allied, was observed by Kölreuter, and more especially by Gärtner, who counted the exact number of seed in each capsule, the two forms were at once ranked as distinct species; and if this rule be followed, assuredly it will never be proved that varieties when crossed are in any degree sterile. We have formerly seen that certain breeds of dogs do not readily pair together; but no observations have been made whether, when paired, they produce the full number of young, and whether the latter are perfectly fertile *inter se*; but, supposing that some degree of sterility were found to exist, naturalists would simply infer that these breeds were descended from aboriginally distinct species; and it would be scarcely possible to ascertain whether or not this explanation was the true one.

The Sebright Bantam is much less prolific than any other breed of fowls, and is descended from a cross between two very distinct breeds, recrossed by a third sub-variety. But it would be extremely rash to infer that the loss of fertility was in any manner connected with its crossed origin, for it may with more probability be attributed either to long-continued close interbreeding, or to an innate tendency to sterility correlated with the absence of hackles and sickle tail-feathers.

Before giving the few recorded cases of forms, which must be ranked as varieties, being in some degree sterile when crossed, I may remark that other causes sometimes interfere with varieties freely intercrossing. Thus they may differ too greatly in size, as with some kinds of dogs and fowls: for instance, the editor of the 'Journal of Horticulture, &c.,'[215] says that he can keep Bantams with the larger breeds without much danger of their crossing, but not with the smaller breeds, such as Games, Hamburgs, &c. With plants a difference in the period of flowering serves to keep varieties distinct, as with the various kinds of maize and wheat: thus Colonel Le Couteur[216] remarks, "the Talavera wheat, from flowering much earlier than any other kind, is sure to continue pure." In different parts of the Falkland {102} Islands the cattle are breaking up into herds of different colours; and those on the higher ground, which are generally white, usually breed, as I am informed by Admiral Sulivan, three months earlier than those on the lowlands; and this would manifestly tend to keep the herds from blending.

Certain domestic races seem to prefer breeding with their own kind; and this is a fact of some importance, for it is a step towards that instinctive feeling which helps to keep closely allied species in a state of nature distinct. We have now abundant evidence that, if it were not for this feeling, many more hybrids would be naturally produced than is the case. We have seen in the first chapter that the alco dog of Mexico dislikes dogs of other breeds; and the hairless dog of Paraguay mixes less readily with the European races, than the latter do with each other. In Germany the female Spitz-dog is said to receive the fox more readily than will other dogs; a female Australian Dingo in England attracted the wild male foxes. But these differences in the sexual instinct and attractive power of the various breeds may be wholly due to their descent from distinct species. In Paraguay the horses have much freedom, and an excellent observer[217] believes that the native horses of the same colour and size prefer associating with each other, and that the horses which have been imported from Entre Rios and Banda Oriental into Paraguay likewise prefer associating together. In Circassia six sub-races of the horse are known and have received distinct names; and a native proprietor of rank[218] asserts that horses of three of these races, whilst living a free life, almost always refuse to mingle and cross, and will even attack each other.

It has been observed, in a district stocked with heavy Lincolnshire and light Norfolk sheep, that both kinds, though bred together, when turned out, "in a short time separate to a sheep;" the Lincolnshires drawing off to the rich soil, and the Norfolks to their own dry light soil; and as long as there is plenty of grass, "the two breeds keep themselves as distinct as rooks and pigeons." In this case different habits of life tend to keep the races distinct. On one of {103} the Faroe islands, not more than half a mile in diameter, the half-wild native black sheep are said not to have readily mixed with the imported white sheep. It is a more curious fact that the semi-monstrous ancon sheep of modern origin "have been observed to keep together, separating themselves from the rest of the flock, when put into enclosures with other sheep."[219] With respect to fallow deer, which live in a semi-domesticated condition, Mr. Bennett[220] states that the dark and pale coloured herds, which have long been kept together in the Forest of Dean, in High Meadow Woods, and in the New Forest, have never been known to mingle: the dark-coloured deer, it may be added, are believed to have been first brought by James I. from Norway, on account of their greater hardiness. I imported from the island of Porto Santo two of the feral rabbits, which differ, as described in the fourth chapter, from common rabbits; both proved to be males, and, though they lived during some years in the Zoological Gardens, the superintendent, Mr. Bartlett, in vain endeavoured to make them breed with various tame kinds; but whether this refusal to breed was due to any change in instinct, or simply to their extreme wildness; or whether confinement had rendered them sterile, as often occurs, cannot be told.

Whilst matching for the sake of experiment many of the most distinct breeds of pigeons, it frequently appeared to me that the birds, though faithful to their marriage vow, retained

some desire after their own kind. Accordingly I asked Mr. Wicking, who has kept a larger stock of various breeds together than any man in England, whether he thought that they would prefer pairing with their own kind, supposing that there were males and females enough of each; and he without hesitation answered that he was convinced that this was the case. It has often been noticed that the dovecot pigeon seems to have an actual aversion towards the several fancy breeds;[221] yet all have certainly sprung from a common progenitor. The Rev. W. D. Fox informs me that his flocks of white and common Chinese geese kept distinct. {104}

These facts and statements, though some of them are incapable of proof, resting only on the opinion of experienced observers, show that some domestic races are led by different habits of life to keep to a certain extent separate, and that others prefer coupling with their own kind, in the same manner as species in a state of nature, though in a much less degree.

With respect to sterility from the crossing of domestic races, I know of no well-ascertained case with animals. This fact, seeing the great difference in structure between some breeds of pigeons, fowls, pigs, dogs, &c., is extraordinary, in contrast with the sterility of many closely allied natural species when crossed; but we shall hereafter attempt to show that it is not so extraordinary as it at first appears. And it may be well here to recall to mind that the amount of external difference between two species will not safely guide us in foretelling whether or not they will breed together, —some closely allied species when crossed being utterly sterile, and others which are extremely unlike being moderately fertile. I have said that no case of sterility in crossed races rests on satisfactory evidence; but here is one which at first seems trustworthy. Mr. Youatt,[222] and a better authority cannot be quoted, states, that formerly in Lancashire crosses were frequently made between longhorn and shorthorn cattle; the first cross was excellent, but the produce was uncertain; in the third or fourth generation the cows were bad milkers; "in addition to which, there was much uncertainty whether the cows would conceive; and full one-third of the cows among some of these half-breds failed to be in calf." This at first seems a good case; but Mr. Wilkinson states,[223] that a breed derived from this same cross was actually established in another part of England; and if it had failed in fertility, the fact would surely have been noticed. Moreover, supposing that Mr. Youatt had proved his case, it might be argued that the sterility was wholly due to the two parent-breeds being descended from primordially distinct species.

I will give a case with plants, to show how difficult it is to get sufficient evidence. Mr. Sheriff, who has been so successful in the formation of new races of wheat, fertilised the Hopetoun with the Talavera; in the first and second generations the produce was intermediate in character, but in the fourth generation "it was found to consist of many varieties; nine-tenths of the florets proved barren, and many of the seeds seemed shrivelled abortions, void of vitality, and the whole race was evidently verging to extinction."[224] Now, considering how little these varieties of wheat differ in any important character, it seems to me very improbable that the sterility resulted, as Mr. Sheriff thought, from the cross, but from some quite distinct cause. Until such experiments are many times repeated, it would be rash to trust them; but unfortunately they have been rarely tried even once with sufficient care. {105}

Gärtner has recorded a more remarkable and trustworthy case: he fertilised thirteen panicles (and subsequently nine others) on a dwarf maize bearing yellow seed[225] with pollen of a tall maize having red seed; and one head alone produced good seed, only five in number. Though these plants are monœcious, and therefore do not require castration, yet I should have suspected some accident in the manipulation had not Gärtner expressly stated that he had during many years grown these two varieties

together, and they did not spontaneously cross; and this, considering that the plants are monœcious and abound with pollen, and are well known generally to cross freely, seems explicable only on the belief that these two varieties are in some degree mutually infertile. The hybrid plants raised from the above five seed were intermediate in structure, extremely variable, and perfectly fertile.[226] No one, I believe, has hitherto suspected that these varieties of maize are distinct species; but had the hybrids been in the least sterile, no doubt Gärtner would at once have so classed them. I may here remark, that with undoubted species there is not necessarily any close relation between the sterility of a first cross and that of the hybrid offspring. Some species can be crossed with facility, but produce utterly sterile hybrids; others can be crossed with extreme difficulty, but the hybrids when produced are moderately fertile. I am not aware, however, of any instance quite like this of the maize with natural species, namely, of a first cross made with difficulty, but yielding perfectly fertile hybrids.

The following case is much more remarkable, and evidently perplexed Gärtner, whose strong wish it was to draw a broad line of distinction between species and varieties. In the genus Verbascum, he made, during eighteen years, a vast number of experiments, and crossed no less than 1085 flowers and counted their seeds. Many of these experiments consisted in crossing white and yellow varieties of both *V. lychnitis* and *V. blattaria* with nine other species and their hybrids. That the white and yellow flowered plants of these two species are really varieties, no one has doubted; and Gärtner actually raised in the case of both species one variety from the seed of the other. Now in two of his works[227] he distinctly asserts that crosses between similarly-coloured flowers yield more seed than between dissimilarly-coloured; so that the yellow-flowered variety of either species (and conversely with the white-flowered variety), when crossed with pollen of its own kind, yields more seed than when crossed with that of the white variety; and so it is when differently coloured species are crossed. The general results may be seen in the Table at the end of his {106} volume. In one instance he gives[228] the following details; but I must premise that Gärtner, to avoid exaggerating the degree of sterility in his crosses, always compares the *maximum* number obtained from a cross with the *average* number naturally given by the pure mother-plant. The white-variety of *V. lychnitis*, naturally fertilised by its own pollen, gave from an *average* of twelve capsules ninety-six good seeds in each; whilst twenty flowers fertilised with pollen from the yellow variety of this same species, gave as the *maximum* only eighty-nine good seed; so that we have the proportion of 1000 to 908, according to Gärtner's usual scale. I should have thought it possible that so small a difference in fertility might have been accounted for by the evil effects of the necessary castration; but Gärtner shows that the white variety of *V. lychnitis*, when fertilised first by the white variety of *V. blattaria*, and then by the yellow variety of this species, yielded seed in the proportion of 622 to 438; and in both these cases castration was performed. Now the sterility which results from the crossing of the differently coloured varieties of the same species, is fully as great as that which occurs in many cases when distinct species are crossed. Unfortunately Gärtner compared the results of the first unions alone, and not the sterility of the two sets of hybrids produced from the white variety of *V. lychnitis* when fertilised by the white and yellow varieties of *V. blattaria*, for it is probable that they would have differed in this respect.

Mr. J. Scott has given me the results of a series of experiments on Verbascum, made by him in the Botanic Gardens of Edinburgh. He repeated some of Gärtner's experiments on distinct species, but obtained only fluctuating results; some confirmatory, but the greater number contradictory; nevertheless these seem hardly sufficient to overthrow the conclusions arrived at by Gärtner from experiments tried

on a much larger scale. In the second place Mr. Scott experimented on the relative fertility of unions between similarly and dissimilarly-coloured varieties of the same species. Thus he fertilised six flowers of the yellow variety of *V. lychnitis* by its own pollen, and obtained six capsules, and calling, for the sake of having a standard of comparison, the average number of good seed in each one hundred, he found that this same yellow variety, when fertilised by the white variety, yielded from seven capsules an average of ninety-four seed. On the same principle, the white variety of *V. lychnitis* by its own pollen (from six capsules), and by the pollen of the yellow variety (eight capsules), yielded seed in the proportion of 100 to 82. The yellow variety of *V. thapsus* by its own pollen (eight capsules), and by that of the white variety (only two capsules), yielded seed in the proportion of 100 to 94. Lastly, the white variety of *V. blattaria* by its own pollen (eight capsules), and by that of the yellow variety (five capsules), yielded seed in the proportion of 100 to 79. So that in every case the unions of dissimilarly-coloured varieties of the same species were less fertile than the unions of similarly-coloured varieties; when all the cases are grouped together, the difference of fertility is as 86 to 100. Some additional trials were made, and altogether thirty-six similarly-coloured unions yielded thirty-five good capsules; whilst thirty-five {107}
dissimilarly-coloured unions yielded only twenty-six good capsules. Besides the foregoing experiments, the purple *V. phœniceum* was crossed by a rose-coloured and a white variety of the same species; these two varieties were also crossed together, and these several unions yielded less seed than *V. phœniceum* by its own pollen. Hence it follows from Mr. Scott's experiments, that in the genus Verbascum the similarly and dissimilarly-coloured varieties of the same species behave, when crossed, like closely allied but distinct species.[229]

This remarkable fact of the sexual affinity of similarly-coloured varieties, as observed by Gärtner and Mr. Scott, may not be of very rare occurrence; for the subject has not been attended to by others. The following case is worth giving, partly to show how difficult it is to avoid error. Dr. Herbert[230] has remarked that variously-coloured double varieties of the hollyhock (*Althæa rosea*) may be raised with certainty by seed from plants growing close together. I have been informed that nurserymen who raise seed for sale do not separate their plants; accordingly I procured seed of eighteen named varieties; of these, eleven varieties produced sixty-two plants all perfectly true to their kind; and seven produced forty-nine plants, half of which were true and half false. Mr. Masters of Canterbury has given me a more striking case; he saved seed from a great bed of twenty-four named varieties planted in closely adjoining rows, and each variety reproduced itself truly with only sometimes a shade of difference in tint. Now in the hollyhock the pollen, which is abundant, is matured and nearly all shed before the stigma of the same flower is ready to receive it;[231] and as bees covered with pollen incessantly fly from plant to plant, it would appear that adjoining varieties could not escape being crossed. As, however, this does not occur, it appeared to me probable that the pollen of each variety was prepotent on its own stigma over {108}
that of all other varieties. But Mr. C. Turner of Slough, well known for his success in the cultivation of this plant, informs me that it is the doubleness of the flowers which prevents the bees gaining access to the pollen and stigma; and he finds that it is difficult even to cross them artificially. Whether this explanation will fully account for varieties in close proximity propagating themselves so truly by seed, I do not know.

The following cases are worth giving, as they relate to monœcious forms, which do not require, and consequently have not been injured by, castration. Girou de Buzareingues crossed what he designates three varieties of gourd,[232] and asserts that their mutual fertilisation is less easy in proportion to the difference which they present. I am aware how imperfectly the forms in this group were until recently known; but Sageret,[233] who ranked them according to their mutual fertility,

considers the three forms above alluded to as varieties, as does a far higher authority, namely, M. Naudin.[234] Sageret[235] has observed that certain melons have a greater tendency, whatever the cause may be, to keep true than others; and M. Naudin, who has had such immense experience in this group, informs me that he believes that certain varieties intercross more readily than others of the same species; but he has not proved the truth of this conclusion; the frequent abortion of the pollen near Paris being one great difficulty. Nevertheless, he has grown close together, during seven years, certain forms of Citrullus, which, as they could be artificially crossed with perfect facility and produced fertile offspring, are ranked as varieties; but these forms when not artificially crossed kept true. Many other varieties, on the other hand, in the same group cross with such facility, as M. Naudin repeatedly insists, that without being grown far apart they cannot be kept in the least true.

Another case, though somewhat different, may be here given, as it is highly remarkable, and is established on excellent evidence. Kölreuter minutely describes five varieties of the common tobacco,[236] which were reciprocally crossed, and the offspring were intermediate in character and as fertile as their parents: from this fact Kölreuter inferred that they are really varieties; and no one, as far as I can discover, seems to have doubted that such is the case. He also crossed reciprocally these five varieties with *N. glutinosa*, and they yielded very sterile hybrids; but those raised from the *var. perennis*, whether used as the father or mother plant, were not so sterile as the hybrids from the four other varieties.[237] So that the sexual capacity of this one variety has certainly been in some degree modified, so as to approach in nature that of *N. glutinosa*.[238] {109}

These facts with respect to plants show that in some few cases certain varieties have had their sexual powers so far modified, that they cross together less readily and yield less seed than other varieties of the same species. We shall presently see that the sexual functions of most animals and plants are eminently liable to be affected by the conditions of life to which they are exposed; and hereafter we shall briefly discuss the conjoint bearing of this and other facts on the difference in fertility between crossed varieties and crossed species.

Domestication eliminates the tendency to Sterility which is general with Species when crossed.

This hypothesis was first propounded by Pallas,[239] and has been adopted by several authors. I can find hardly any direct facts in its support; but unfortunately no one has compared, in the case of either animals or plants, the fertility of anciently domesticated varieties, when crossed with a distinct species, with that of the wild parent-species when similarly crossed. No one has compared, for instance, the fertility of *Gallus bankiva* and of the domesticated fowl, when crossed with a distinct species of Gallus or Phasianus; and the experiment would in all cases be surrounded by many difficulties. Dureau de la Malle, who has so closely studied classical literature, states[240] that in the time of the Romans the common mule was produced with more difficulty than at the present day; but whether this statement may be trusted I know not. A much more important, though somewhat different, case is given by M. Groenland,[241] namely, that plants, known from their intermediate character and sterility to be hybrids between Ægilops and wheat, have perpetuated themselves under culture since 1857, *with a rapid but varying increase of fertility in each generation*. In the fourth generation the plants, still retaining their intermediate character, had become as fertile as common cultivated wheat. {110}

The indirect evidence in favour of the Pallasian doctrine appears to me to be extremely strong. In the earlier chapters I have attempted to show that our various breeds of dogs are descended from several wild species; and this probably is the case with sheep. There can no

longer be any doubt that the Zebu or humped Indian ox belongs to a distinct species from European cattle: the latter, moreover, are descended from two or three forms, which may be called either species or wild races, but which co-existed in a state of nature and kept distinct. We have good evidence that our domesticated pigs belong to at least two specific types, *S. scrofa* and *Indica*, which probably lived together in a wild state in South-eastern Europe. Now, a widely-extended analogy leads to the belief that if these several allied species, in the wild state or when first reclaimed, had been crossed, they would have exhibited, both in their first unions and in their hybrid offspring, some degree of sterility. Nevertheless the several domesticated races descended from them are now all, as far as can be ascertained, perfectly fertile together. If this reasoning be trustworthy, and it is apparently sound, we must admit the Pallasian doctrine that long-continued domestication tends to eliminate that sterility which is natural to species when crossed in their aboriginal state.

On increased Fertility from Domestication and Cultivation. {111}

Increased fertility from domestication, without any reference to crossing, may be here briefly considered. This subject bears indirectly on two or three points connected with the modification of organic beings. As Buffon long ago remarked,[242] domestic animals breed oftener in the year and produce more young at a birth than wild animals of the same species; they, also, sometimes breed at an earlier age. The case would hardly have deserved further notice, had not some authors lately attempted to show that fertility increases and decreases in an inverse ratio with the amount of food. This strange doctrine has apparently arisen from individual animals when supplied with an inordinate quantity of food, and from plants of many kinds when grown on excessively rich soil, as on a dunghill, becoming sterile; but to this latter point I shall have occasion presently to return. With hardly an exception, our domesticated animals, which have long been habituated to a regular and copious supply of food, without the labour of searching for it, are more fertile than the corresponding wild animals. It is notorious how frequently cats and dogs breed, and how many young they produce at a birth. The wild rabbit is said generally to breed four times yearly, and to produce from four to eight young; the tame rabbit breeds six or seven times yearly, and produces from four to eleven young. The ferret, though generally so closely confined, is more prolific than its supposed wild prototype. The wild sow is remarkably prolific, for she often breeds twice in the year, and produces from four to eight and sometimes even twelve young at a birth; but the domestic sow regularly breeds twice a year, and would breed oftener if permitted; and a sow that produces less than eight at a birth "is worth little, and the sooner she is fattened for the butcher the better." The amount of food affects the fertility even of the same individual: thus sheep, which on mountains never produce more than one lamb at a birth, when brought down to lowland pastures frequently bear twins. This {112} difference apparently is not due to the cold of the higher land, for sheep and other domestic animals are said to be extremely prolific in Lapland. Hard living, also, retards the period at which animals conceive; for it has been found disadvantageous in the northern islands of Scotland to allow cows to bear calves before they are four years old.[243]

Birds offer still better evidence of increased fertility from domestication: the hen of the wild *Gallus bankiva* lays from six to ten eggs, a number which would be thought nothing of with the domestic hen. The wild duck lays from five to ten eggs; the tame one in the course of the year from eighty to one hundred. The wild grey-lag goose lays from five to eight eggs; the tame from thirteen to eighteen, and she lays a second time; as Mr. Dixon has remarked, "high-feeding, care, and moderate warmth induce a habit of prolificacy which becomes in some measure hereditary." Whether the semi-domesticated dovecot pigeon is more fertile than the wild rock-pigeon *C. livia*, I know not; but the more thoroughly domesticated breeds are nearly twice as fertile as dovecots: the latter, however, when caged and highly fed, become equally fertile with house pigeons. The peahen alone of domesticated birds is rather more fertile,

according to some accounts, when wild in its native Indian home, than when domesticated in Europe and exposed to our much colder climate.[244]

With respect to plants, no one would expect wheat to tiller more, and each ear to produce more grain, in poor than in rich soil; or to get in poor soil a heavy crop of peas or beans. Seeds vary so much in number that it is difficult to estimate them; but {113}
on comparing beds of carrots saved for seed in a nursery garden with wild plants, the former seemed to produce about twice as much seed. Cultivated cabbages yielded thrice as many pods by measure as wild cabbages from the rocks of South Wales. The excess of berries produced by the cultivated Asparagus in comparison with the wild plant is enormous. No doubt many highly cultivated plants, such as pears, pineapples, bananas, sugar-cane, &c., are nearly or quite sterile; and I am inclined to attribute this sterility to excess of food and to other unnatural conditions; but to this subject I shall presently recur.

In some cases, as with the pig, rabbit, &c., and with those plants which are valued for their seed, the direct selection of the more fertile individuals has probably much increased their fertility; and in all cases this may have occurred indirectly, from the better chance of the more numerous offspring produced by the more fertile individuals having survived. But with cats, ferrets, and dogs, and with plants like carrots, cabbages, and asparagus, which are not valued for their prolificacy, selection can have played only a subordinate part; and their increased fertility must be attributed to the more favourable conditions of life under which they have long existed.

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CHAPTER XVII.

ON THE GOOD EFFECTS OF CROSSING, AND ON THE EVIL EFFECTS OF CLOSE INTERBREEDING.

DEFINITION OF CLOSE INTERBREEDING—AUGMENTATION OF MORBID TENDENCIES—GENERAL EVIDENCE ON THE GOOD EFFECTS DERIVED FROM CROSSING, AND ON THE EVIL EFFECTS FROM CLOSE INTERBREEDING—CATTLE, CLOSELY INTERBRED; HALF-WILD CATTLE LONG KEPT IN THE SAME PARKS—SHEEP—FALLOW-DEER—DOGS—RABBITS—PIGS—MAN, ORIGIN OF HIS ABHORRENCE OF INCESTUOUS MARRIAGES—FOWLS—PIGEONS—HIVE-BEES—PLANTS, GENERAL CONSIDERATIONS ON THE BENEFITS DERIVED FROM CROSSING—MELONS, FRUIT-TREES, PEAS, CABBAGES, WHEAT, AND FOREST-TREES—ON THE INCREASED SIZE OF HYBRID PLANTS, NOT EXCLUSIVELY DUE TO THEIR STERILITY—ON CERTAIN PLANTS WHICH EITHER NORMALLY OR ABNORMALLY ARE SELF-IMPOTENT, BUT ARE FERTILE, BOTH ON THE MALE AND FEMALE SIDE, WHEN CROSSED WITH DISTINCT INDIVIDUALS EITHER OF THE SAME OR ANOTHER SPECIES—CONCLUSION.

The gain in constitutional vigour, derived from an occasional cross between individuals of the same variety, but belonging to distinct families, or between distinct varieties, has not been so largely or so frequently discussed, as have the evil effects of too close interbreeding. But the former point is the more important of the two, inasmuch as the evidence is more decisive. The evil results from close interbreeding are difficult to detect, for they accumulate slowly, and differ much in degree with different species; whilst the good effects which almost invariably follow a cross are from the first manifest. It should, however, be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigour. In relation to the subject of domestication, the whole question is of some importance, as too close interbreeding interferes with the improvement of old

races, and especially with the formation of new ones. It is important as indirectly bearing on Hybridism; and perhaps on the extinction of species, when any form has become so rare that only a few individuals remain within a confined area. It bears in an important manner on the {115} influence of free intercrossing, in obliterating individual differences, and thus giving uniformity of character to the individuals of the same race or species; for if additional vigour and fertility be thus gained, the crossed offspring will multiply and prevail, and the ultimate result will be far greater than otherwise would have occurred. Lastly, the question is of high interest, as bearing on mankind. Hence I shall discuss this subject at full length. As the facts which prove the evil effects of close interbreeding are more copious, though less decisive, than those on the good effects of crossing, I shall, under each group of beings, begin with the former.

There is no difficulty in defining what is meant by a cross; but this is by no means easy in regard to "breeding in and in" or "too close interbreeding," because, as we shall see, different species of animals are differently affected by the same degree of interbreeding. The pairing of a father and daughter, or mother and son, or brothers and sisters, if carried on during several generations, is the closest possible form of interbreeding. But some good judges, for instance Sir J. Sebright, believe that the pairing of a brother and sister is closer than that of parents and children; for when the father is matched with his daughter he crosses, as is said, with only half his own blood. The consequences of close interbreeding carried on for too long a time, are, as is generally believed, loss of size, constitutional vigour, and fertility, sometimes accompanied by a tendency to malformation. Manifest evil does not usually follow from pairing the nearest relations for two, three, or even four generations; but several causes interfere with our detecting the evil—such as the deterioration being very gradual, and the difficulty of distinguishing between such direct evil and the inevitable augmentation of any morbid tendencies which may be latent or apparent in the related parents. On the other hand, the benefit from a cross, even when there has not been any very close interbreeding, is almost invariably at once conspicuous. There is reason to believe, and this was the opinion of that most experienced observer Sir J. Sebright,[245] that the evil effects of close interbreeding may be checked by the related individuals being separated during a few generations and exposed to different conditions of {116} life.

That evil directly follows from any degree of close interbreeding has been denied by many persons; but rarely by any practical breeder; and never, as far as I know, by one who has largely bred animals which propagate their kind quickly. Many physiologists attribute the evil exclusively to the combination and consequent increase of morbid tendencies common to both parents: that this is an active source of mischief there can be no doubt. It is unfortunately too notorious that men and various domestic animals endowed with a wretched constitution, and with a strong hereditary disposition to disease, if not actually ill, are fully capable of procreating their kind. Close interbreeding, on the other hand, induces sterility; and this indicates something quite distinct from the augmentation of morbid tendencies common to both parents. The evidence immediately to be given convinces me that it is a great law of nature, that all organic beings profit from an occasional cross with individuals not closely related to them in blood; and that, on the other hand, long-continued close interbreeding is injurious.

Various general considerations have had much influence in leading me to this conclusion; but the reader will probably rely more on special facts and opinions. The authority of experienced observers, even when they do not advance the grounds of their belief, is of some little value. Now almost all men who have bred many kinds of animals and have written on the subject, such as Sir J. Sebright, Andrew Knight, &c.,[246] have expressed the strongest conviction on the impossibility of long-continued close interbreeding. Those who have compiled works on agriculture, and have associated much with breeders, such as the sagacious Youatt, Low, &c., have strongly declared their opinion to the same effect. Prosper

Lucas, trusting largely to French authorities, has come to a similar conclusion. The distinguished German agriculturist Hermann von Nathusius, who has written the most able treatise on this subject which I have met with, concurs; and as I shall have to quote from this treatise, I may state that Nathusius is not only intimately acquainted with works on {117} agriculture in all languages, and knows the pedigrees of our British breeds better than most Englishmen, but has imported many of our improved animals, and is himself an experienced breeder.

Evidence of the evil effects of close interbreeding can most readily be acquired in the case of animals, such as fowls, pigeons, &c., which propagate quickly, and, from being kept in the same place, are exposed to the same conditions. Now I have inquired of very many breeders of these birds, and I have hitherto not met with a single man who was not thoroughly convinced that an occasional cross with another strain of the same sub-variety was absolutely necessary. Most breeders of highly-improved or fancy birds value their own strain, and are most unwilling, at the risk, in their opinion, of deterioration, to make a cross. The purchase of a first-rate bird of another strain is expensive, and exchanges are troublesome; yet all breeders, as far as I can hear, excepting those who keep large stocks at different places for the sake of crossing, are driven after a time to take this step.

Another general consideration which has had great influence on my mind is, that with all hermaphrodite animals and plants, which it might have been thought would have perpetually fertilised themselves, and thus have been subjected for long ages to the closest interbreeding, there is no single species, as far as I can discover, in which the structure ensures self-fertilisation. On the contrary, there are in a multitude of cases, as briefly stated in the fifteenth chapter, manifest adaptations which favour or inevitably lead to an occasional cross between one hermaphrodite and another of the same species; and these adaptive structures are utterly purposeless, as far as we can see, for any other end.

With *Cattle* there can be no doubt that extremely close interbreeding may be long carried on, advantageously with respect to external characters and with no manifestly apparent evil as far as constitution is concerned. The same remark is applicable to sheep. Whether these animals have gradually been rendered less susceptible than others to this evil, in order to permit them to live in herds,—a habit which leads the old and vigorous males to expel all intruders, and in consequence often to pair with their own daughters, I will not pretend to decide. The case of Bakewell's Long-horns, which were closely interbred for a long period, has often been quoted; yet Youatt {118} says[247] the breed "had acquired a delicacy of constitution inconsistent with common management," and "the propagation of the species was not always certain." But the Shorthorns offer the most striking case of close interbreeding; for instance, the famous bull Favourite (who was himself the offspring of a half-brother and sister from Foljambe) was matched with his own daughter, granddaughter, and great-granddaughter; so that the produce of this last union, or the great-great-granddaughter, had 15-16ths, or 93.75 per cent. of the blood of Favourite in her veins. This cow was matched with the bull Wellington, having 62.5 per cent. of Favourite blood in his veins, and produced Clarissa; Clarissa was matched with the bull Lancaster, having 68.75 of the same blood, and she yielded valuable offspring.[248] Nevertheless Collings, who reared these animals, and was a strong advocate for close breeding, once crossed his stock with a Galloway, and the cows from this cross realised the highest prices. Bates's herd was esteemed the most celebrated in the world. For thirteen years he bred most closely in and in; but during the next seventeen years, though he had the most exalted notion of the value of his own stock, he thrice infused fresh blood into his herd: it is said that he did this, not to improve the form of his animals, but on account of their lessened fertility. Mr. Bates's own view, as given by a celebrated breeder,[249] was, that "to breed in and in from a bad stock was ruin and

devastation; yet that the practice may be safely followed within certain limits when the parents so related are descended from first-rate animals." We thus see that there has been extremely close interbreeding with Shorthorns; but Nathusius, after the most careful study of their pedigrees, says that he can find no instance of a breeder who has strictly followed this practice during his whole life. From this study and his own experience, he concludes that close interbreeding is necessary to ennoble the stock; but that in effecting this the greatest care is necessary, on account of the tendency to infertility and weakness. It may be added, that another high authority[250] asserts that many more calves are born cripples from Shorthorns than from other and less closely interbred races of cattle.

Although by carefully selecting the best animals (as Nature effectually does by the law of battle) close interbreeding may be long carried on with cattle, yet the good effects of a cross between almost any two breeds is at once shown by the greater size and vigour of the offspring; as Mr. Spooner writes to me, "crossing distinct breeds certainly improves cattle for the butcher." Such crossed animals are of course of no value to the breeder; but they have been raised during many years in several parts of {119} England to be slaughtered;[251] and their merit is now so fully recognised, that at fat-cattle shows a separate class has been formed for their reception. The best fat ox at the great show at Islington in 1862 was a crossed animal.

The half-wild cattle, which have been kept in British parks probably for 400 or 500 years, or even for a longer period, have been advanced by Culley and others as a case of long-continued interbreeding within the limits of the same herd without any consequent injury. With respect to the cattle at Chillingham, the late Lord Tankerville owned that they were bad breeders.[252] The agent, Mr. Hardy, estimates (in a letter to me, dated May, 1861) that in the herd of about fifty the average number annually slaughtered, killed by fighting, and dying, is about ten, or one in five. As the herd is kept up to nearly the same average number, the annual rate of increase must be likewise about one in five. The bulls, I may add, engage in furious battles, of which battles the present Lord Tankerville has given me a graphic description, so that there will always be rigorous selection of the most vigorous males. I procured in 1855 from Mr. D. Gardner, agent to the Duke of Hamilton, the following account of the wild cattle kept in the Duke's park in Lanarkshire, which is about 200 acres in extent. The number of cattle varies from sixty-five to eighty; and the number annually killed (I presume by all causes) is from eight to ten; so that the annual rate of increase can hardly be more than one in six. Now in South America, where the herds are half-wild, and therefore offer a nearly fair standard of comparison, according to Azara the natural increase of the cattle on an estancia is from one-third to one-fourth of the total number, or one in between three and four; and this, no doubt, applies exclusively to adult animals fit for consumption. Hence the half-wild British cattle which have long interbred within the limits of the same herd are relatively far less fertile. Although in an unenclosed country like Paraguay there must be some crossing between the different herds, yet even there the inhabitants believe that the occasional introduction of animals from distant localities is necessary to prevent "degeneration in size and diminution of fertility."[253] The decrease in size from ancient times in the Chillingham and Hamilton cattle must have been prodigious, for Professor Rütimeyer has shown that they are almost certainly the descendants of the gigantic *Bos primigenius*. No doubt this decrease in size may be largely attributed to less favourable conditions of life; yet animals roaming over large parks, and fed during severe winters, can hardly be considered as placed under very unfavourable conditions.

With *Sheep* there has often been long-continued interbreeding within the limits of the same flock; but whether the nearest relations have been matched so frequently as in the case of Shorthorn cattle, I do not know. The Messrs. Brown during fifty years have never infused fresh blood into their excellent flock of Leicesters. Since 1810 Mr. Barford has acted on the same principle with the Foscote flock. He asserts that half a century of experience has convinced him that when two nearly related animals are {120} quite sound in constitution, in-and-in breeding does not induce degeneracy; but he adds that he "does not pride himself on breeding from the nearest affinities." In France the Naz flock has been bred for sixty years without the introduction of a single strange ram.[254] Nevertheless, most great breeders of sheep have protested against close interbreeding prolonged for too great a length of time.[255] The most celebrated of recent breeders, Jonas Webb, kept five separate families to work on, thus "retaining the requisite distance of relationship between the sexes."[256]

Although by the aid of careful selection the near interbreeding of sheep may be long continued without any manifest evil, yet it has often been the practice with farmers to cross distinct breeds to obtain animals for the butcher, which plainly shows that good is derived from this practice. Mr. Spooner sums up his excellent Essay on Crossing by asserting that there is a direct pecuniary advantage in judicious cross-breeding, especially when the male is larger than the female. A former celebrated breeder, Lord Somerville, distinctly states that his half-breeds from Ryelands and Spanish sheep were larger animals than either the pure Ryelands or pure Spanish sheep.[257]

As some of our British parks are ancient, it occurred to me that there must have been long-continued close interbreeding with the fallow deer (*Cervus dama*) kept in them; but on inquiry I find that it is a common practice to infuse new blood by procuring bucks from other parks. Mr. Shirley,[258] who has carefully studied the management of deer, admits that in some parks there has been no admixture of foreign blood from a time beyond the memory of man. But he concludes "that in the end the constant breeding in-and-in is sure to tell to the disadvantage of the whole herd, though it may take a very long time to prove it; moreover, when we find, as is very constantly the case, that the introduction of fresh blood has been of the very greatest use to deer, both by improving their size and appearance, and particularly by being of service in removing the taint of 'rickback,' if not of other diseases, to which deer are sometimes subject when the blood has not been changed, there can, I think, be no doubt but that a judicious cross with a good stock is of the greatest consequence, and is indeed essential, sooner or later, to the prosperity of every well-ordered park."

Mr. Meynell's famous foxhounds have been adduced, as showing that no ill effects follow from close interbreeding; and Sir J. Sebright ascertained from him that he frequently bred from father and daughter, mother and son, and sometimes even from {121} brothers and sisters. Sir J. Sebright, however, declares,[259] that by breeding *in-and-in*, by which he means matching brothers and sisters, he has actually seen strong spaniels become weak and diminutive lapdogs. The Rev. W. D. Fox has communicated to me the case of a small lot of bloodhounds, long kept in the same family, which had become very bad breeders, and nearly all had a bony enlargement in the tail. A single cross with a distinct strain of bloodhounds restored their fertility, and drove away the tendency to malformation in the tail. I have heard the particulars of another case with bloodhounds, in which the female had to be held to the male. Considering how rapid is the natural increase of the dog, it is difficult to understand the high price of most highly improved breeds, which almost implies long-continued close interbreeding, except on the belief that this process lessens fertility and increases liability to distemper and other diseases. A high authority, Mr. Scrope, attributes the rarity and

deterioration in size of the Scotch deerhound (the few individuals now existing throughout the country being all related) in large part to close interbreeding.

With all highly-bred animals there is more or less difficulty in getting them to procreate quickly, and all suffer much from delicacy of constitution; but I do not pretend that these effects ought to be wholly attributed to close interbreeding. A great judge of rabbits[260] says, "the long-eared does are often too highly bred or forced in their youth to be of much value as breeders, often turning out barren or bad mothers." Again: "Very long-eared bucks will also sometimes prove barren." These highly-bred rabbits often desert their young, so that it is necessary to have nurse-rabbits.

With *Pigs* there is more unanimity amongst breeders on the evil effects of close interbreeding than, perhaps, with any other large animal. Mr. Druce, a great and successful breeder of the Improved Oxfordshires (a crossed race), writes, "without a change of boars of a different tribe, but of the same breed, constitution cannot be preserved." Mr. Fisher Hobbs, the raiser of the celebrated Improved Essex breed, divided his stock into three separate families, by which means he maintained the breed for more than twenty years, "by judicious selection from the *three distinct families*."[261] Lord Western was the first importer of a Neapolitan boar and sow. "From this pair he bred in-and-in, until the breed was in danger of becoming extinct, a sure result (as Mr. Sidney remarks) of in-and-in breeding." Lord Western then crossed his Neapolitan pigs with the old Essex, and made the first great step towards the Improved Essex breed. Here is a more interesting case. Mr. J. Wright, well known as a breeder, crossed[262] the same boar with the daughter, granddaughter, and great-granddaughter, and so on for seven generations. The result was, that in many instances the offspring failed to breed; in others they produced few that lived; and of the latter many were idiotic, without sense even to suck, and when attempting to move could not walk straight. Now it deserves especial notice, that the two last sows produced by this long course of interbreeding were sent to other boars, and they bore several litters of healthy pigs. The best sow in external appearance produced during the whole seven generations was one in the last stage of descent; but the litter consisted of this one sow. She would not breed to her sire, yet bred at the first trial to a stranger in blood. So that, in Mr. Wright's case, long-continued and extremely close interbreeding did not affect the external form or merit of the young; but with many of them the general constitution and mental powers, and especially the reproductive functions, were seriously affected. {122}

Nathusius gives[263] an analogous and even more striking case: he imported from England a pregnant sow of the large Yorkshire breed, and bred the product closely in-and-in for three generations: the result was unfavourable, as the young were weak in constitution, with impaired fertility. One of the latest sows, which he esteemed a good animal, produced, when paired with her own uncle (who was known to be productive with sows of other breeds), a litter of six, and a second time a litter of only five weak young pigs. He then paired this sow with a boar of a small black breed, which he had likewise imported from England, and which boar, when matched with sows of his own breed, produced from seven to nine young: now, the sow of the large breed, which was so unproductive when paired with her own uncle, yielded to the small black boar, in the first litter twenty-one, and in the second litter eighteen young pigs; so that in one year she produced thirty-nine fine young animals!

As in the case of several other animals already mentioned, even when no injury is perceptible from moderately close interbreeding, yet, to quote the words of Mr. Coate, a most successful breeder (who five times won the annual gold medal of the Smithfield Club Show for the best pen of pigs), "Crosses answer well for profit to the

farmer, as you get more constitution and quicker growth; but for me, who sell a great number of pigs for breeding purposes, I find it will not do, as it requires many years to get anything like purity of blood again."[264]

Before passing on to Birds, I ought to refer to man, though I am unwilling to enter on this subject, as it is surrounded by natural prejudices. It has moreover been discussed by various authors under many points of view.[265] Mr. Tylor[266] has shown that with widely different {123}
races, in the most distant quarters of the world, marriages between relations—even between distant relations—have been strictly prohibited. A few exceptional cases can be specified, especially with royal families; and these have been enlarged on in a learned article[267] by Mr. W. Adam, and formerly in 1828 by Hofacker. Mr. Tylor is inclined to believe that the almost universal prohibition of closely-related marriages has arisen from their evil effects having been observed, and he ingeniously explains some apparent anomalies in the prohibition not extending equally to the relations on both the male and female side. He admits, however, that other causes, such as the extension of friendly alliances, may have come into play. Mr. W. Adam, on the other hand, concludes that related marriages are prohibited and viewed with repugnance from the confusion which would thus arise in the descent of property, and from other still more recondite reasons; but I cannot accept this view, seeing that the savages of Australia and South America,[268] who have no property to bequeath or fine moral feelings to confuse, hold the crime of incest in abhorrence.

It would be interesting to know, if it could be ascertained, as throwing light on this question with respect to man, what occurs with the higher anthropomorphous apes—whether the young males and females soon wander away from their parents, or whether the old males become jealous of their sons and expel them, or whether any inherited instinctive feeling, from being beneficial, has been generated, leading the young males and females of the same family to prefer pairing with distinct families, and to dislike pairing with each other. A considerable body of evidence has already been advanced, showing that the offspring from parents which are not related are more vigorous and fertile than those from parents which are closely related; hence any slight feeling, arising from the sexual excitement of novelty or other cause, which led to the former rather than to the latter unions, would be augmented through natural selection, and thus might become instinctive; for those individuals which had an innate preference of this kind would increase in number. It seems more probable, that degraded savages should thus unconsciously have acquired their dislike and even {124}
abhorrence of incestuous marriages, rather than that they should have discovered by reasoning and observation the evil results. The abhorrence occasionally failing is no valid argument against the feeling being instinctive, for any instinct may occasionally fail or become vitiated, as sometimes occurs with parental love and the social sympathies. In the case of man, the question whether evil follows from close interbreeding will probably never be answered by direct evidence, as he propagates his kind so slowly and cannot be subjected to experiment; but the almost universal practice of all races at all times of avoiding closely-related marriages is an argument of considerable weight; and whatever conclusion we arrive at in regard to the higher animals may be safely extended to man.

Turning now to Birds: in the case of the *Fowl* a whole array of authorities could be given against too close interbreeding. Sir J. Sebright positively asserts that he made many trials, and that his fowls, when thus treated, became long in the legs, small in the body, and bad breeders.[269] He produced the famous Sebright Bantams by complicated crosses, and by breeding in-and-in; and since his time there has been much close interbreeding with these Bantams; and they are now notoriously bad breeders. I have seen Silver Bantams, directly descended from his stock, which had become almost as barren as hybrids; for not a single chicken had been that year hatched from two full nests of eggs. Mr. Hewitt says that with these Bantams the

sterility of the male stands, with rare exceptions, in the closest relation with their loss of certain secondary male characters: he adds, "I have noticed, as a general rule, that even the slightest deviation from feminine character in the tail of the male Sebright—say the elongation by only half an inch of the two principal tail-feathers—brings with it improved probability of increased fertility."[270]

Mr. Wright states[271] that Mr. Clark, "whose fighting-cocks were so notorious, continued to breed from his own kind till they lost their disposition to fight, but stood to be cut up without making any resistance, and were so reduced in size as to be under those weights required for the best prizes; but on obtaining a cross from Mr. Leighton, they again resumed their former courage and weight." It should be borne in mind that game-cocks before they fought were always weighed, so that nothing was left to the imagination about any reduction or increase of weight. Mr. Clark does not seem to {125}
have bred from brothers and sisters, which is the most injurious kind of union; and he found, after repeated trials, that there was a greater reduction in weight in the young from a father paired with his daughter, than from a mother with her son. I may add that Mr. Eyton, of Eyton, the well-known ornithologist, who is a large breeder of Grey Dorkings, informs me that they certainly diminish in size, and become less prolific, unless a cross with another strain is occasionally obtained. So it is with Malays, according to Mr. Hewitt, as far as size is concerned.[272]

An experienced writer[273] remarks that the same amateur, as is well known, seldom long maintains the superiority of his birds; and this, he adds, undoubtedly is due to all his stock "being of the same blood;" hence it is indispensable that he should occasionally procure a bird of another strain. But this is not necessary with those who keep a stock of fowls at different stations. Thus, Mr. Ballance, who has bred Malays for thirty years, and has won more prizes with these birds than any other fancier in England, says that breeding in-and-in does not necessarily cause deterioration; "but all depends upon how this is managed." "My plan has been to keep about five or six distinct runs, and to rear about two hundred or three hundred chickens each year, and select the best birds from each run for crossing. I thus secure sufficient crossing to prevent deterioration."[274]

We thus see that there is almost complete unanimity with poultry-breeders that, when fowls are kept at the same place, evil quickly follows from interbreeding carried on to an extent which would be disregarded in the case of most quadrupeds. On the other hand, it is a generally received opinion that cross-bred chickens are the hardiest and most easily reared.[275] Mr. Tegetmeier, who has carefully attended to poultry of all breeds, says[276] that Dorking hens, allowed to run with Houdan or Crevecœur cocks, "produce in the early spring chickens that for size, hardihood, early maturity, and fitness for the market, surpass those of any pure breed that we have ever raised." Mr. Hewitt gives it as a general rule with fowls, that crossing the breed increases their size. He makes this remark after stating that hybrids from the pheasant and fowl are considerably larger than either progenitor: so again, hybrids from the male golden pheasant and hen common pheasant "are of far larger size than either parent-bird." [277] To this subject of the increased size of hybrids I shall presently return.

With *Pigeons*, breeders are unanimous, as previously stated, that it is absolutely indispensable, notwithstanding the trouble and expense thus caused, occasionally to cross their much-prized birds with individuals of another strain, but belonging, of course, to the same variety. It deserves notice that, when large size is one of the {126}
desired characters, as with pouters,[278] the evil effects of close interbreeding are much sooner perceived than when small birds, such as short-faced tumblers, are

valued. The extreme delicacy of the high fancy breeds, such as these tumblers and improved English carriers, is remarkable; they are liable to many diseases, and often die in the egg or during the first moult; and their eggs have generally to be hatched under foster-mothers. Although these highly-prized birds have invariably been subjected to much close interbreeding, yet their extreme delicacy of constitution cannot perhaps be thus fully explained. Mr. Yarrell informed me that Sir J. Sebright continued closely interbreeding some owl-pigeons, until from their extreme sterility he as nearly as possible lost the whole family. Mr. Brent[279] tried to raise a breed of trumpeters, by crossing a common pigeon, and recrossing the daughter, granddaughter, great-granddaughter, and great-great-granddaughter, with the same male trumpeter, until he obtained a bird with $^{15}/_{16}$ths of trumpeter's blood; but then the experiment failed, for "breeding so close stopped reproduction." The experienced Neumeister[280] also asserts that the offspring from dovecotes and various other breeds are "generally very fertile and hardy birds:" so again, MM. Boitard and Corbié, [281] after forty-five years' experience, recommend persons to cross their breeds for amusement; for, if they fail to make interesting birds, they will succeed under an economical point of view, "as it is found that mongrels are more fertile than pigeons of pure race."

I will refer only to one other animal, namely, the Hive-bee, because a distinguished entomologist has advanced this as a case of inevitable close interbreeding. As the hive is tenanted by a single female, it might have been thought that her male and female offspring would always have bred together, more especially as bees of different hives are hostile to each other; a strange worker being almost always attacked when trying to enter another hive. But Mr. Tegetmeier has shown[282] that this instinct does not apply to drones, which are permitted to enter any hive; so that there is no *à priori* improbability of a queen receiving a foreign drone. The fact of the union invariably and necessarily taking place on the wing, during the queen's nuptial flight, seems to be a special provision against continued interbreeding. However this may be, experience has shown, since the introduction of the yellow-banded Ligurian race into Germany and England, that bees freely cross: Mr. Woodbury, who introduced Ligurian bees into Devonshire, found during a single season that three stocks, at distances of from one to two miles from his hives, were crossed by his drones. In one case the Ligurian drones must have flown over the city of Exeter, and over several intermediate hives. On another occasion several common black queens were crossed by Ligurian drones at a distance of from one to three and a half miles.[283]

Plants. {127}

When a single plant of a new species is introduced into any country, if propagated by seed, many individuals will soon be raised, so that if the proper insects be present there will be crossing. With newly-introduced trees or other plants not propagated by seed we are not here concerned. With old-established plants it is an almost universal practice occasionally to make exchanges of seed, by which means individuals which have been exposed to different conditions of life,—and this, as we have seen, diminishes the evil from close interbreeding,—will occasionally be introduced into each district.

Experiments have not been tried on the effects of fertilising flowers with their own pollen during *several* generations. But we shall presently see that certain plants, either normally or abnormally, are more or less sterile, even in the first generation, when fertilised by their own pollen. Although nothing is directly known on the evil effects

of long-continued close interbreeding with plants, the converse proposition that great good is derived from crossing is well established.

With respect to the crossing of individuals belonging to the same sub-variety, Gärtner, whose accuracy and experience exceeded that of all other hybridisers, states[284] that he has many times observed good effects from this step, especially with exotic genera, of which the fertility is somewhat impaired, such as Passiflora, Lobelia, and Fuchsia. Herbert also says,[285] "I am inclined to think that I have derived advantage from impregnating the flower from which I wished to obtain seed with pollen from another individual of the same variety, or at least from another flower, rather than with its own." Again, Professor Lecoq asserts that he has ascertained that crossed offspring are more vigorous and robust than their parents.[286]

General statements of this kind, however, can seldom be fully trusted; consequently I have begun a series of experiments, which, if they continue to give the same results as hitherto, will for ever settle the question of the good effects of crossing two distinct plants of the same variety, and of the evil effects of self-fertilisation. A clear light will thus also be thrown on the fact that flowers are invariably constructed so as to permit, or favour, or necessitate the union of two individuals. We shall clearly understand why monœcious and diœcious,—why dimorphic and trimorphic plants exist, and many other such cases. The plan which I have followed in my experiments is to grow plants in the same pot, or in pots of the same size, or close together in the open ground; to carefully exclude insects; and then to fertilise some of the flowers with pollen from the same flower, and others on the same plant with pollen from a distinct but adjoining plant. In many, but not all, of these experiments, the crossed plants yielded much more seed than the self-fertilised plants; and I have never seen the reversed case. The self-fertilised and crossed seeds thus obtained were allowed to germinate in the same glass vessel on damp sand; and as the seeds successively germinated, they were planted in pairs on opposite sides of the same pot, with a superficial partition between them, and were placed so as to be equally exposed to the light. In other cases the self-fertilised and crossed seeds were simply sown on opposite sides of the same small pot. I have, in short, followed different plans, but in every case have taken all the precautions which I could think of, so that the two lots should be equally favoured. Now, I have carefully observed the growth of plants raised from crossed and self-fertilised seed, from their germination to maturity, in species of the following genera, namely, Brassica, Lathyrus, Lupinus, Lobelia, Lactuca, Dianthus, Myosotis, Petunia, Linaria, Calceolaria, Mimulus, and Ipomœa, and the difference in their powers of growth, and of withstanding in certain cases unfavourable conditions, was most manifest and strongly marked. It is of importance that the two lots of seed should be sown or planted on opposite sides of the same pot, so that the seedlings may struggle against each other; for if sown separately in ample and good soil, there is often but little difference in their growth. {128}

I will briefly describe the two most striking cases as yet observed by me. Six crossed and six self-fertilised seeds of *Ipomœa purpurea*, from plants treated in the manner above described, were planted as soon as they had germinated, in pairs on opposite sides of two pots, and rods of equal thickness were given them to twine up. Five of the crossed plants grew from the first more quickly than the opposed self-fertilised plants; the sixth, however, was weakly and was for a time beaten, but at last its sounder constitution prevailed and it shot ahead of its antagonist. As soon as each crossed plant reached the top of its seven-foot rod its fellow was measured, and the result was that, when the crossed plants were seven feet high, the self-fertilised had attained the average height of only five feet four and a half inches. The crossed plants flowered a little before, and more profusely than the self-fertilised plants. On opposite sides of

another *small* pot a large number of crossed and self-fertilised seeds were sown, so that they had to struggle for bare existence; a single rod was given to each lot: here again the crossed plants showed from the first their advantage; they never quite reached the summit of the seven-foot rod, but relatively to the self-fertilised plants their average height was as seven feet to five feet two inches. The experiment was repeated in the two following generations with plants raised from the self-fertilised and crossed plants, treated in exactly the same manner, and with nearly the same result. In the second generation, the crossed plants, which were again crossed, produced 121 seed-capsules, whilst the self-fertilised plants, again self-fertilised, produced only 84 capsules.

Some flowers of the *Mimulus luteus* were fertilised with their own pollen, and others were crossed with pollen from distinct plants growing in the same pot. The seeds after germinating were thickly planted on opposite sides of a pot. The seedlings were at first equal in height; but when the young crossed plants were exactly half an inch, the self-fertilised plants were only a quarter of an inch high. But this inequality did not {129}
continue, for, when the crossed plants were four and a half inches high, the self-fertilised were three inches; and they retained the same relative difference till their growth was complete. The crossed plants looked far more vigorous than the uncrossed, and flowered before them; they produced also a far greater number of flowers, which yielded capsules (judging, however, from only a few) containing more seeds. As in the former case, the experiment was repeated in the same manner during the next two generations, and with exactly the same result. Had I not watched these plants of the Mimulus and Ipomœa during their whole growth, I could not have believed it possible, that a difference apparently so slight, as that of the pollen being taken from the same flower, and from a distinct plant growing in the same small pot, could have made so wonderful a difference in the growth and vigour of the plants thus produced. This, under a physiological point of view, is a most remarkable phenomenon.

With respect to the benefit derived from crossing distinct varieties, plenty of evidence has been published. Sageret[287] repeatedly speaks in strong terms of the vigour of melons raised by crossing different varieties, and adds that they are more easily fertilised than common melons, and produce numerous good seed. Here follows the evidence of an English gardener:[288] "I have this summer met with better success in my cultivation of melons, in an unprotected state, from the seeds of hybrids (*i.e.* mongrels) obtained by cross impregnation, than with old varieties. The offspring of three different hybridisations (one more especially, of which the parents were the two most dissimilar varieties I could select) each yielded more ample and finer produce than any one of between twenty and thirty established varieties."

Andrew Knight[289] believed that his seedlings from crossed varieties of the apple exhibited increased vigour and luxuriance; and M. Chevreul[290] alludes to the extreme vigour of some of the crossed fruit-trees raised by Sageret.

By crossing reciprocally the tallest and shortest peas, Knight[291] says, "I had in this experiment a striking instance of the stimulative effects of crossing the breeds; for the smallest variety, whose height rarely exceeded two feet, was increased to six feet; whilst the height of the large and luxuriant kind was very little diminished." Mr. Laxton gave me seed-peas produced from crosses between four distinct kinds; and the plants thus raised were extraordinarily vigorous, being in each case from one to two or three feet taller than the parent-forms growing close alongside them.

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Wiegmann[292] made many crosses between several varieties of cabbage; and he speaks with astonishment of the vigour and height of the mongrels, which excited the amazement of all the gardeners who beheld them. Mr. Chaundy raised a great number of mongrels by planting together six distinct varieties of cabbage. These mongrels displayed an infinite diversity of character; "But the most remarkable circumstance was, that, while all the other cabbages and borecoles in the nursery were destroyed by a severe winter, these hybrids were little injured, and supplied the kitchen when there was no other cabbage to be had."

Mr. Maund exhibited before the Royal Agricultural Society[293] specimens of crossed wheat, together with their parent varieties; and the editor states that they were intermediate in character, "united with that greater vigour of growth, which it appears, in the vegetable as in the animal world, is the result of a first cross." Knight also crossed several varieties of wheat,[294] and he says "that in the years 1795 and 1796, when almost the whole crop of corn in the island was blighted, the varieties thus obtained, and these only, escaped in this neighbourhood, though sown in several different soils and situations."

Here is a remarkable case: M. Clotzsch[295] crossed *Pinus sylvestris* and *nigricans*, *Quercus robur* and *pedunculata, Alnus glutinosa* and *incana*, *Ulmus campestris* and *effusa*; and the cross-fertilised seeds, as well as seeds of the pure parent-trees, were all sown at the same time and in the same place. The result was, that after an interval of eight years, the hybrids were one-third taller than the pure trees!

The facts above given refer to undoubted varieties, excepting the trees crossed by Clotzsch, which are ranked by various botanists as strongly-marked races, sub-species, or species. That true hybrids raised from entirely distinct species, though they lose in fertility, often gain in size and constitutional vigour, is certain. It would be superfluous to quote any facts; for all experimenters, Kölreuter, Gärtner, Herbert, Sageret, Lecoq, and Naudin, have been struck with the wonderful vigour, height, size, tenacity of life, precocity, and hardiness of their hybrid productions. Gärtner[296] sums up his conviction on this head in the strongest terms. Kölreuter[297] gives numerous precise measurements of the weight and height of his hybrids in comparison with measurements of both parent-forms; and speaks with astonishment of their "*statura portentosa*," their "*ambitus vastissimus ac altitudo valde conspicua*." Some exceptions to the rule in the case of very sterile hybrids have, however, been noticed by Gärtner and Herbert; but the most striking exceptions are given by Max Wichura, {131} [298] who found that hybrid willows were generally tender in constitution, dwarf, and short-lived.

Kölreuter explains the vast increase in the size of the roots, stems, &c., of his hybrids, as the result of a sort of compensation due to their sterility, in the same way as many emasculated animals are larger than the perfect males. This view seems at first sight extremely probable, and has been accepted by various authors;[299] but Gärtner[300] has well remarked that there is much difficulty in fully admitting it; for with many hybrids there is no parallelism between the degree of their sterility and their increased size and vigour. The most striking instances of luxuriant growth have been observed with hybrids which were not sterile in any extreme degree. In the genus Mirabilis, certain hybrids are unusually fertile, and their extraordinary luxuriance of growth, together with their enormous roots,[301] have been transmitted to their progeny. The increased size of the hybrids produced between the fowl and pheasant, and between the distinct species of pheasants, has been already noticed. The result in all cases is probably in part due to the saving of nutriment and vital force through the sexual

organs not acting, or acting imperfectly, but more especially to the general law of good being derived from a cross. For it deserves especial attention that mongrel animals and plants, which are so far from being sterile that their fertility is often actually augmented, have, as previously shown, their size, hardiness, and constitutional vigour generally increased. It is not a little remarkable that an accession of vigour and size should thus arise under the opposite contingencies of increased and diminished fertility.

It is a perfectly well ascertained fact[302] that hybrids will invariably breed more readily with either pure parent, and not rarely with a distinct species, than with each other. Herbert is inclined to explain even this fact by the advantage derived from a cross; but Gärtner more justly accounts for it by the pollen of the hybrid, and probably its ovules, being in some degree vitiated, whereas the pollen and ovules of both pure parents and of any third species are sound. Nevertheless there are some well-ascertained and remarkable facts, which, as we shall immediately see, show that the act of crossing in itself undoubtedly tends to increase or re-establish the fertility of hybrids.

On certain Hermaphrodite Plants which, either normally or abnormally, require to be fertilised by pollen from a distinct individual or species.

The facts now to be given differ from those hitherto detailed, as the self-sterility does not here result from long-continued, close interbreeding. These facts are, however, connected {132} with our present subject, because a cross with a distinct individual is shown to be either necessary or advantageous. Dimorphic and trimorphic plants, though they are hermaphrodites, must be reciprocally crossed, one set of forms by the other, in order to be fully fertile, and in some cases to be fertile in any degree. But I should not have noticed these plants, had it not been for the following cases given by Dr. Hildebrand:[303]—

Primula sinensis is a reciprocally dimorphic species: Dr. Hildebrand fertilised twenty-eight flowers of both forms, each by pollen of the other form, and obtained the full number of capsules containing on an average 42.7 seed per capsule; here we have complete and normal fertility. He then fertilised forty-two flowers of both forms with pollen of the same form, but taken from a distinct plant, and all produced capsules containing on an average only 19.6 seed. Lastly, and here we come to our more immediate point, he fertilised forty-eight flowers of both forms with pollen of the same form, taken from the same flower, and now he obtained only thirty-two capsules, and these contained on an average 18.6 seed, or one less per capsule than in the former case. So that, with these illegitimate unions, the act of impregnation is less assured, and the fertility slightly less, when the pollen and ovules belong to the same flower, than when belonging to two distinct individuals of the same form. Dr. Hildebrand has recently made analogous experiments on the long-styled form of *Oxalis rosea*, with the same result.[304]

It has recently been discovered that certain plants, whilst growing in their native country under natural conditions, cannot be fertilised with pollen from the same plant. They are sometimes so utterly self-impotent, that, though they can readily be fertilised by the pollen of a distinct species or even distinct genus, yet, wonderful as the fact is, they never produce a single seed by their own pollen. In some cases, moreover, the plant's own pollen and stigma mutually act on each other in a deleterious manner. Most of the facts to be given relate to Orchids, but I will commence with a plant belonging to a widely different family.

Sixty-three flowers of *Corydalis cava*, borne on distinct plants, were fertilised by Dr. Hildebrand[305] with pollen from other plants of the same species; and fifty-eight

capsules were obtained, including on an average 4.5 seed in each. He then fertilised sixteen flowers produced by the same raceme, one with another, but obtained only three capsules, one of which alone contained any good seeds, namely, two in number. Lastly, he fertilised twenty-seven flowers, each with its own pollen; he left also fifty-seven flowers to be spontaneously fertilised, and this would certainly have ensued if it had been possible, for the anthers not only touch the stigma, but the pollen-tubes were seen by Dr. Hildebrand to penetrate it; nevertheless these eighty-four flowers did not produce a single seed-capsule! This whole case is highly instructive, as it shows how widely different the action of the same pollen is, according as it is placed on the stigma of the same flower, or on that of another flower on the same raceme, or on that of a distinct plant. {133}

With exotic Orchids several analogous cases have been observed, chiefly by Mr. John Scott.[306] *Oncidium sphacelatum* has effective pollen, for with it Mr. Scott fertilised two distinct species; its ovules are likewise capable of impregnation, for they were readily fertilised by the pollen of *O. divaricatum*; nevertheless, between one and two hundred flowers fertilised by their own pollen did not produce a single capsule, though the stigmas were penetrated by the pollen-tubes. Mr. Robinson Munro, of the Royal Botanic Gardens of Edinburgh, also informs me (1864) that a hundred and twenty flowers of this same species were fertilised by him with their own pollen, and did not produce a capsule, but eight flowers fertilised by the pollen of *O. divaricatum* produced four fine capsules: again, between two and three hundred flowers of *O. divaricatum*, fertilised by their own pollen, did not set a capsule, but twelve flowers fertilised by *O. flexuosum* produced eight fine capsules: so that here we have three utterly self-impotent species, with their male and female organs perfect, as shown by their mutual fertilisation. In these cases fertilisation was effected only by the aid of a distinct species. But, as we shall presently see, distinct plants, raised from seed, of *Oncidium flexuosum*, and probably of the other species, would have been perfectly capable of fertilising each other, for this is the natural process. Again, Mr. Scott found that the pollen of a plant of *O. microchilum* was good, for with it he fertilised two distinct species; he found its ovules good, for they could be fertilised by the pollen of one of these species, and by the pollen of a distinct plant of *O. microchilum*; but they could not be fertilised by pollen of the same plant, though the pollen-tubes penetrated the stigma. An analogous case has been recorded by M. Rivière,[307] with two plants of *O. Cavendishianum*, which were both self-sterile, but reciprocally fertilised each other. All these cases refer to the genus Oncidium, but Mr. Scott found that *Maxillaria atro-rubens* was "totally insusceptible of fertilisation with its own pollen," but fertilised, and was fertilised by, a widely distinct species, viz. *M. squalens*.

As these orchids had grown under unnatural conditions, in hot-houses, I concluded without hesitation that their self-sterility was due to this cause. But Fritz Müller informs me that at Desterro, in Brazil, he fertilised above one hundred flowers of the above-mentioned *Oncidium flexuosum*, which is there endemic, with its own pollen, and with that taken from distinct plants; all the former were sterile, whilst those fertilised by pollen from any *other plant* of the same species were fertile. During the first three days there was no difference in the action of the two kinds of pollen: that placed on the stigma of the same plant separated in the usual manner into grains, and emitted tubes which penetrated the column, and the stigmatic chamber shut itself; but the flowers alone which had been fertilised by pollen taken from a distinct plant produced seed-capsules. On a subsequent occasion these experiments were repeated on a large scale with the same result. Fritz Müller found that four other endemic species of Oncidium were in like manner utterly sterile with their own pollen, but fertile with that from any other plant: some of them likewise produced seed-capsules when impregnated with pollen of widely distinct genera, such as Leptotes, {134}

Cyrtopodium, and Rodriguezia! *Oncidium crispum*, however, differs from the foregoing species in varying much in its self-sterility; some plants producing fine pods with their own pollen, others failing to do so; in two or three instances, Fritz Müller observed that the pods produced by pollen taken from a distinct flower on the same plant, were larger than those produced by the flower's own pollen. In *Epidendrum cinnabarinum*, an orchid belonging to another division of the family, fine pods were produced by the plant's own pollen, but they contained by weight only about half as much seed as the capsules which had been fertilized by pollen from a distinct plant, and in one instance from a distinct species; moreover, a very large proportion, and in some cases nearly all the seed produced by the plant's own pollen, was embryonless and worthless. Some self-fertilized capsules of a Maxillaria were in a similar state.

Another observation made by Fritz Müller is highly remarkable, namely, that with various orchids the plant's own pollen not only fails to impregnate the flower, but acts on the stigma, and is acted on, in an injurious or poisonous manner. This is shown by the surface of the stigma in contact with the pollen, and by the pollen itself, becoming in from three to five days dark brown, and then decaying. The discolouration and decay are not caused by parasitic cryptogams, which were observed by Fritz Müller in only a single instance. These changes are well shown by placing on the same stigma, at the same time, the plant's own pollen and that from a distinct plant of the same species, or of another species, or even of another and widely remote genus. Thus, on the stigma of *Oncidium flexuosum*, the plant's own pollen and that from a distinct plant were placed side by side, and in five days' time the latter was perfectly fresh, whilst the plant's own pollen was brown. On the other hand, when the pollen of a distinct plant of the *Oncidium flexuosum*, and of the *Epidendrum zebra* (*nov. spec.?*), were placed together on the same stigma, they behaved in exactly the same manner, the grains separating, emitting tubes, and penetrating the stigma, so that the two pollen-masses, after an interval of eleven days, could not be distinguished except by {135} the difference of their caudicles, which, of course, undergo no change. Fritz Müller has, moreover, made a large number of crosses between orchids belonging to distinct species and genera, and he finds that in all cases when the flowers are not fertilised their footstalks first begin to wither; and the withering slowly spreads upwards until the germens fall off, after an interval of one or two weeks, and in one instance of between six and seven weeks; but even in this latter case, and in most other cases, the pollen and stigma remained in appearance fresh. Occasionally, however, the pollen becomes brownish, generally on the external surface, and not in contact with the stigma, as is invariably the case when the plant's own pollen is applied.

Fritz Müller observed the poisonous action of the plant's own pollen in the above-mentioned *Oncidium flexuosum*, *O. unicorne, pubes* (*?*), and in two other unnamed species. Also in two species of Rodriguezia, in two of Notylia, in one of Burlingtonia, and of a fourth genus in the same group. In all these cases, except the last, it was proved that the flowers were, as might have been expected, fertile with pollen from a distinct plant of the same species. Numerous flowers of one species of Notylia were fertilized with pollen from the same raceme; in two days' time they all withered, the germens began to shrink, the pollen-masses became dark brown, and not one pollen-grain emitted a tube. So that in this orchid the injurious action of the plant's own pollen is more rapid than with *Oncidium flexuosum*. Eight other flowers on the same raceme were fertilized with pollen from a distinct plant of the same species: two of these were dissected, and their stigmas were found to be penetrated by numberless pollen-tubes; and the germens of the other six flowers became well developed. On a subsequent occasion many other flowers were fertilized with their own pollen, and all fell off dead in a few days; whilst some flowers on the same raceme which had been left simply unfertilised adhered and long remained fresh. We have seen that in cross-

unions between extremely distinct orchids the pollen long remains undecayed; but Notylia behaved in this respect differently; for when its pollen was placed on the stigma of *Oncidium flexuosum*, both the stigma and pollen quickly became dark brown, in the same manner as if the plant's own pollen had been applied.

Fritz Müller suggests that, as in all these cases the plant's own pollen is not only impotent (thus effectually preventing self-fertilization), but likewise prevents, as was ascertained in the case of the Notylia and *Oncidium flexuosum*, the action of subsequently applied pollen from a distinct individual, it would be an advantage to the plant to have its own pollen rendered more and more deleterious; for the germens would thus quickly be killed, and, dropping off, there would be no further waste in nourishing a part which ultimately could be of no avail. Fritz Müller's discovery that a plant's own pollen and stigma in some cases act on each other as if mutually poisonous, is certainly most remarkable.

We now come to cases closely analogous with those just given, but different, inasmuch as {136} individual plants alone of the species are self-impotent. This self-impotence does not depend on the pollen or ovules being in a state unfit for fertilisation, for both have been found effective in union with other plants of the same or of a distinct species. The fact of these plants having spontaneously acquired so peculiar a constitution, that they can be fertilised more readily by the pollen of a distinct species than by their own, is remarkable. These abnormal cases, as well as the foregoing normal cases, in which certain orchids, for instance, can be much more easily fertilised by the pollen of a distinct species than by their own, are exactly the reverse of what occurs with all ordinary species. For in these latter the two sexual elements of the same individual plant are capable of freely acting on each other; but are so constituted that they are more or less impotent when brought into union with the sexual elements of a distinct species, and produce more or less sterile hybrids. It would appear that the pollen or ovules, or both, of the individual plants which are in this abnormal state, have been affected in some strange manner by the conditions to which they themselves or their parents have been exposed; but whilst thus rendered self-sterile, they have retained the capacity common to most species of partially fertilizing and being partially fertilized by allied forms. However this may be, the subject, to a certain extent, is related to our general conclusion that good is derived from the act of crossing.

Gärtner experimented on two plants of *Lobelia fulgens*, brought from separate places, and found[308] that their pollen was good, for he fertilised with it *L. cardinalis* and *syphilitica*; their ovules were likewise good, for they were fertilised by the pollen of these same two species; but these two plants of *L. fulgens* could not be fertilised by their own pollen, as can generally be effected with perfect ease with this species. Again, the pollen of a plant of *Verbascum nigrum* grown in a pot was found by Gärtner[309] capable of fertilising *V. lychnitis* and *V. Austriacum*; the ovules could be fertilised by the pollen of *V. thapsus*; but the flowers could not be fertilised by their own pollen. Kölreuter, also,[310] gives the case of three garden plants of *Verbascum* {137} *phœniceum*, which bore during two years many flowers; these he successfully fertilised by the pollen of no less than four distinct species, but they produced not a seed with their own apparently good pollen; subsequently these same plants, and others raised from seed, assumed a strangely fluctuating condition, being temporarily sterile on the male or female side, or on both sides, and sometimes fertile on both sides; but two of the plants were perfectly fertile throughout the summer.

It appears[311] that certain flowers on certain plants of *Lilium candidum* can be fertilised more easily by pollen from a distinct individual than by their own. So, again, with the varieties of the potato. Tinzmann,[312] who made many trials with this plant, says that pollen from another variety sometimes "exerts a powerful influence, and I

have found sorts of potatoes which would not bear seed from impregnation with the pollen of their own flowers, would bear it when impregnated with other pollen." It does not, however, appear to have been proved that the pollen which failed to act on the flower's own stigma was in itself good.

In the genus Passiflora it has long been known that several species do not produce fruit, unless fertilised by pollen taken from distinct species: thus, Mr. Mowbray[313] found that he could not get fruit from *P. alata* and *racemosa* except by reciprocally fertilising them with each other's pollen. Similar facts have been observed in Germany and France;[314] and I have received two authentic accounts of *P. quadrangularis*, which never produced fruit with its own pollen, but would do so freely when fertilised in one case with the pollen of *P. cærulea*, and in another case with that of *P. edulis*. So again, with respect to *P. laurifolia*, a cultivator of much experience has recently remarked[315] that the flowers "must be fertilised with the pollen of *P. cærulea*, or of some other common kind, as their own pollen will not fertilise them." But the fullest details on this subject have been given by Mr. Scott:[316] plants of *Passiflora racemosa*, *cærulea*, and *alata* flowered profusely during many years in the Botanic Gardens of Edinburgh, and, though repeatedly fertilised by Mr. Scott and by others with their own pollen, never produced any seed; yet this occurred at once with all three species when they were crossed together in various ways. But in the case of *P. cærulea*, three plants, two of which grew in the Botanic Gardens, were all rendered fertile, merely by impregnating the one with pollen of the other. The same result was attained in the same manner with *P. alata*, but only with one plant out of three. As so many self-sterile species have been mentioned, it may be stated that in the case of *P. gracilis*, which is an annual, the flowers are nearly as fertile with their own pollen as with that from a distinct plant; thus sixteen flowers spontaneously self-fertilised {138} produced fruit, each containing on an average 21.3 seed, whilst fruit from fourteen crossed flowers contained 24.1 seed.

Returning to *P. alata*, I have received (1866) some interesting details from Mr. Robinson Munro. Three plants, including one in England, have already been mentioned which were inveterately self-sterile, and Mr. Munro informs me of several others which, after repeated trials during many years, have been found in the same predicament. At some other places, however, this species fruits readily when fertilised with its own pollen. At Taymouth Castle there is a plant which was formerly grafted by Mr. Donaldson on a distinct species, name unknown, and ever since the operation it has produced fruit in abundance by its own pollen; so that this small and unnatural change in the state of this plant has restored its self-fertility! Some of the seedlings from the Taymouth Castle plant were found to be not only sterile with their own pollen, but with each other's pollen, and with the pollen of distinct species. Pollen from the Taymouth plant failed to fertilise certain plants of the same species, but was successful on one plant in the Edinburgh Botanic Gardens. Seedlings were raised from this latter union, and some of their flowers were fertilised by Mr. Munro with their own pollen; but they were found to be as self-impotent as the mother-plant had always proved, except when fertilised by the grafted Taymouth plant, and except, as we shall see, when fertilised by her own seedlings. For Mr. Munro fertilised eighteen flowers on the self-impotent mother-plant with pollen from these her own self-impotent seedlings, and obtained, remarkable as the fact is, eighteen fine capsules full of excellent seed! I have met with no case in regard to plants which shows so well as this of *P. alata*, on what small and mysterious causes complete fertility or complete sterility depends.

The facts hitherto given relate to the much-lessened or completely destroyed fertility of pure species when impregnated with their own pollen, in comparison with their fertility when

impregnated by distinct individuals or distinct species; but closely analogous facts have been observed with hybrids.

Herbert states[317] that having in flower at the same time nine hybrid Hippeastrums, of complicated origin, descended from several species, he found that "almost every flower touched with pollen from another cross produced seed abundantly, and those which were touched with their own pollen either failed entirely, or formed slowly a pod of inferior size, with fewer seeds." In the 'Horticultural Journal' he adds that, "the admission of the pollen of another cross-bred Hippeastrum (however complicated the cross) to any *one* flower of the number, is almost sure to check the fructification of the others." In a letter written to me in 1839, Dr. Herbert says that he had already tried these experiments during five consecutive years, and he subsequently repeated them, with the same invariable result. He was thus led to make an analogous trial on a pure {139}
species, namely, on the *Hippeastrum aulicum*, which he had lately imported from Brazil: this bulb produced four flowers, three of which were fertilised by their own pollen, and the fourth by the pollen of a triple cross between *H. bulbulosum*, *reginæ*, and *vittatum*; the result was, that "the ovaries of the three first flowers soon ceased to grow, and after a few days perished entirely: whereas the pod impregnated by the hybrid made vigorous and rapid progress to maturity, and bore good seed, which vegetated freely." This is, indeed, as Herbert remarks, "a strange truth," but not so strange as it then appeared.

As a confirmation of these statements, I may add that Mr. M. Mayes,[318] after much experience in crossing the species of Amaryllis (Hippeastrum), says, "neither the species nor the hybrids will, we are well aware, produce seed so abundantly from their own pollen as from that of others." So, again, Mr. Bidwell, in New South Wales,[319] asserts that *Amaryllis belladonna* bears many more seeds when fertilised by the pollen of *Brunswigia* (*Amaryllis* of some authors) *Josephinæ* or of *B. multiflora*, than when fertilised by its own pollen. Mr. Beaton dusted four flowers of a Cyrtanthus with their own pollen, and four with the pollen of *Vallota* (*Amaryllis*) *purpurea*; on the seventh day "those which received their own pollen slackened their growth, and ultimately perished; those which were crossed with the Vallota held on."[320] These latter cases, however, relate to uncrossed species, like those before given with respect to Passiflora, Orchids, &c., and are here referred to only because the plants belong to the same group of Amaryllidaceæ.

In the experiments on the hybrid Hippeastrums, if Herbert had found that the pollen of two or three kinds alone had been more efficient on certain kinds than their own pollen, it might have been argued that these, from their mixed parentage, had a closer mutual affinity than the others; but this explanation is inadmissible, for the trials were made reciprocally backwards and forwards on nine different hybrids; and a cross, whichever way taken, always proved highly beneficial. I can add a striking and analogous case from experiments made by the Rev. A. Rawson, of Bromley Common, with some complex hybrids of Gladiolus. This skilful horticulturist possessed a number of French varieties, differing from each other only in the colour and size of the flowers, all descended from Gandavensis, a well-known old hybrid, said to be descended from *G. Natalensis* by the pollen of *G. oppositiflorus*.[321] Mr. Rawson, after repeated trials, found that none of the varieties would set seed with their own pollen, although taken from distinct plants of the same variety, which had, of course, {140}
been propagated by bulbs, but that they all seeded freely with pollen from any other variety. To give two examples: Ophir did not produce a capsule with its own pollen, but when fertilised with that of Janire, Brenchleyensis, Vulcain, and Linné, it produced ten fine capsules; but the pollen of Ophir was good, for when Linné was fertilised by it seven capsules were produced. This later variety, on the other hand,

was utterly barren with its own pollen, which we have seen was perfectly efficient on Ophir. Altogether, Mr. Rawson, in the year 1861, fertilised twenty-six flowers borne by four varieties with pollen taken from other varieties, and every single flower produced a fine seed-capsule; whereas fifty-two flowers on the same plants, fertilised at the same time with their own pollen, did not yield a single seed-capsule. Mr. Rawson fertilised, in some cases, the alternate flowers, and in other cases all those down one side of the spike, with pollen of other varieties, and the remaining flowers with their own pollen; I saw these plants when the capsules were nearly mature, and their curious arrangement at once brought full conviction to the mind that an immense advantage had been derived from crossing these hybrids.

Lastly, I have heard from Dr. E. Bornet, of Antibes, who has made numerous experiments in crossing the species of Cistus, but as not yet published the results, that, when any of these hybrids are fertile, they may be said to be, in regard to function, diœcious; "for the flowers are always sterile when the pistil is fertilised by pollen taken from the same flower or from flowers on the same plant. But they are often fertile if pollen be employed from a distinct individual of the same hybrid nature, or from a hybrid made by a reciprocal cross."

Conclusion.—The facts just given, which show that certain plants are self-sterile, although both sexual elements are in a fit state for reproduction when united with distinct individuals of the same or other species, appear at first sight opposed to all analogy. The sexual elements of the same flower have become, as already remarked, differentiated in relation to each other, almost like those of two distinct species.

With respect to the species which, whilst living under their natural conditions, have their reproductive organs in this peculiar state, we may conclude that it has been naturally acquired for the sake of effectually preventing self-fertilisation. The case is closely analous with dimorphic and trimorphic plants, which can be fully fertilised only by plants belong to the opposite form, and not, as in the foregoing cases, in differently by any other plant. Some of these dimorphic plants are completely sterile with pollen taken from the same plant or from the same form. It is interesting to observe the graduated series from plants which, {141} when fertilised by their own pollen, yield the full number of seed, but with the seedlings a little dwarfed in stature—to plants which when self-fertilised yield few seeds—to those with yield none—and, lastly, to those in which the plant's own pollen and stigma act on each other like poison. This peculiar state of the reproductive organs, when occurring in certain individuals alone, is evidently abnormal; and as it chiefly affects exotic plants, or indigenous plants cultivated in pots, we may attribute it to some change in the conditions of life, acting on the plants themselves or on their parents. The self-impotent *Passiflora alata*, which recovered its self-fertility after having been grafted on a distinct stock, shows how small a change is sufficient to act powerfully on the reproductive system. The possibility of a plant becoming under culture self-impotent is interesting as throwing light on the occurrence of this same condition in natural species. A cultivated plant in this state generally remains so during its whole life; and from this fact we may infer that the state is probably congenital.

Kölreuter, however, has described some plants of Verbascum which varied in this respect even during the same season. As in all the normal cases, and in many, probably in most, of the abnormal cases, any two self-impotent plants can reciprocally fertilize each other, we may infer that a very slight difference in the nature of their sexual elements suffices to give fertility; but in other instances, as with some Passifloras and the hybrid Gladioli, a greater degree of differentiation appears to be necessary, for with these plants fertility is gained only by the union of distinct species, or of hybrids of distinct parentage. These facts all point to the same general conclusion, namely, that good is derived from a cross between

individuals, which either innately, or from exposure to dissimilar conditions, have come to differ in sexual constitution.

Exotic animals confined in menageries are sometimes in nearly the same state as the above-described self-impotent plants; for, as we shall see in the following chapter, certain monkeys, the larger carnivora, several finches, geese, and pheasants, cross together, quite as freely as, or even more freely than, the individuals of the same species breed together. Cases will, also, be given of sexual incompatibility between certain male and female domesticated {142}
animals, which, nevertheless, are fertile when matched with any other individual of the same kind.

In the early part of this chapter it was shown that the crossing of distinct forms, whether closely or distantly allied, gives increased size and constitutional vigour, and, except in the case of crossed species, increased fertility, to the offspring. The evidence rests on the universal testimony of breeders (for it should be observed that I am not here speaking of the evil results of close interbreeding), and is practically exemplified in the higher value of cross-bred animals for immediate consumption. The good results of crossing have also been demonstrated, in the case of some animals and of numerous plants, by actual weight and measurement. Although animals of pure blood will obviously be deteriorated by crossing, as far as their characteristic qualities are concerned, there seems to be no exception to the rule that advantages of the kind just mentioned are thus gained, even when there has not been any previous close interbreeding. The rule applies to all animals, even to cattle and sheep, which can long resist breeding in-and-in between the nearest blood-relations. It applies to individuals of the same sub-variety but of distinct families, to varieties or races, to sub-species, as well as to quite distinct species.

In this latter case, however, whilst size, vigour, precocity, and hardiness are, with rare exceptions, gained, fertility, in a greater or less degree, is lost; but the gain cannot be exclusively attributed to the principle of compensation; for there is no close parallelism between the increased size and vigour of the offspring and their sterility. Moreover it has been clearly proved that mongrels which are perfectly fertile gain these same advantages as well as sterile hybrids.

The evil consequences of long-continued close interbreeding are not so easily recognised as the good effects from crossing, for the deterioration is gradual. Nevertheless it is the general opinion of those who have had most experience, especially with animals which propagate quickly, that evil does inevitably follow sooner or later, but at different rates with different animals. No doubt a false belief may widely prevail like a superstition; yet it is difficult to suppose that so many acute and original observers have all been deceived at the expense of {143}
much cost and trouble. A male animal may sometimes be paired with his daughter, granddaughter, and so on, even for seven generations, without any manifest bad result; but the experiment has never been tried of matching brothers and sisters, which is considered the closest form of interbreeding, for an equal number of generations. There is good reason to believe that by keeping the members of the same family in distinct bodies, especially if exposed to somewhat different conditions of life, and by occasionally crossing these families, the evil results may be much diminished, or quite eliminated. These results are loss of constitutional vigour, size, and fertility; but there is no necessary deterioration in the general form of the body, or in other good qualities. We have seen that with pigs first-rate animals have been produced after long-continued close interbreeding, though they had become extremely infertile when paired with their near relations. The loss of fertility, when it occurs, seems never to be absolute, but only relative to animals of the same blood; so that this sterility is to a certain extent analogous with that of self-impotent plants which cannot be fertilised by their own pollen, but are perfectly fertile with pollen of any other plant of the same species. The fact of infertility of this peculiar nature being one of the results of long-continued interbreeding, shows that interbreeding does not act merely by combining

and augmenting various morbid tendencies common to both parents; for animals with such tendencies, if not at the time actually ill, can generally propagate their kind. Although offspring descended from the nearest blood-relations are not necessarily deteriorated in structure, yet some authors[322] believe that they are eminently liable to malformations; and this is not improbable, as everything which lessens the vital powers acts in this manner. Instances of this kind have been recorded in the case of pigs, bloodhounds, and some other animals.

Finally, when we consider the various facts now given which plainly show that good follows from crossing, and less plainly that evil follows from close interbreeding, and when we bear in mind that throughout the whole organic world elaborate provision has been made for the occasional union of distinct individuals, the existence of a great law of nature is, if not proved, at least rendered in the highest degree probable; namely, that the crossing of animals and plants which are not closely related to beach other is highly beneficial or even necessary, and that interbreeding prolonged during many generations is highly injurious. {144}

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CHAPTER XVIII.

ON THE ADVANTAGES AND DISADVANTAGES OF CHANGED CONDITIONS OF LIFE: STERILITY FROM VARIOUS CAUSES.

ON THE GOOD DERIVED FROM SLIGHT CHANGES IN THE CONDITIONS OF LIFE—STERILITY FROM CHANGED CONDITIONS, IN ANIMALS, IN THEIR NATIVE COUNTRY AND IN MENAGERIES—MAMMALS, BIRDS, AND INSECTS—LOSS OF SECONDARY SEXUAL CHARACTERS AND OF INSTINCTS—CAUSES OF STERILITY—STERILITY OF DOMESTICATED ANIMALS FROM CHANGED CONDITIONS—SEXUAL INCOMPATIBILITY OF INDIVIDUAL ANIMALS—STERILITY OF PLANTS FROM CHANGED CONDITIONS OF LIFE—CONTABESCENCE OF THE ANTHERS—MONSTROSITIES AS A CAUSE OF STERILITY—DOUBLE FLOWERS—SEEDLESS FRUIT—STERILITY FROM THE EXCESSIVE DEVELOPMENT OF THE ORGANS OF VEGETATION—FROM LONG-CONTINUED PROPAGATION BY BUDS—INCIPIENT STERILITY THE PRIMARY CAUSE OF DOUBLE FLOWERS AND SEEDLESS FRUIT.

On the Good derived from slight Changes in the Conditions of Life.—In considering whether any facts were known which might throw light on the conclusion arrived at in the last chapter, namely, that benefits ensue from crossing, and that it is a law of nature that all organic beings should occasionally cross, it appeared to me probable that the good derived from slight changes in the conditions of life, from being an analogous phenomenon, might serve this purpose. No two individuals, and still less no two varieties, are absolutely alike in constitution and structure; and when the germ of one is fertilised by the male element of another, we may believe that it is acted on in a somewhat similar manner as an individual when exposed to slightly changed conditions. Now, every one must have observed the remarkable influence on convalescents of a change of residence, and no medical man doubts the truth of this fact. Small farmers who hold but little land are convinced that their cattle derive great benefit from a change of pasture. In the case of plants, the evidence is strong that a great advantage is derived from exchanging seeds, tubers, bulbs, and cuttings from one soil or place to another as different as possible. {146}

The belief that plants are thus benefited, whether or not well founded, has been firmly maintained from the time of Columella, who wrote shortly after the Christian era, to the present day; and it now prevails in England, France, and Germany.[323] A sagacious observer, Bradley, writing in 1724,[324] says, "When we once become Masters of a good Sort of Seed, we should at least put it into Two or Three Hands,

where the Soils and Situations are as different as possible; and every Year the Parties should change with one another; by which Means, I find the Goodness of the Seed will be maintained for several Years. For Want of this Use many Farmers have failed in their Crops and been great Losers." He then gives his own practical experience on this head. A modern writer[325] asserts, "Nothing can be more clearly established in agriculture than that the continual growth of any one variety in the same district makes it liable to deterioration either in quality or quantity." Another writer states that he sowed close together in the same field two lots of wheat-seed, the product of the same original stock, one of which had been grown on the same land, and the other at a distance, and the difference in favour of the crop from the latter seed was remarkable. A gentleman in Surrey who has long made it his business to raise wheat to sell for seed, and who has constantly realised in the market higher prices than others, assures me that he finds it indispensable continually to change his seed; and that for this purpose he keeps two farms differing much in soil and elevation.

With respect to the tubers of the potato, I find that at the present day the practice of exchanging sets is almost everywhere followed. The great growers of potatoes in Lancashire formerly used to get tubers from Scotland, but they found that "a change from the moss-lands, and *vice versâ*, was generally sufficient." In former times in France the crop of potatoes in the Vosges had become reduced in the course of fifty or sixty years in the proportion from 120-150 to 30-40 bushels; and the famous Oberlin attributed the surprising good which he effected in large part to changing the sets.[326]

A well-known practical gardener, Mr. Robson[327] positively states that he has himself witnessed decided advantage from obtaining bulbs of the onion, tubers of the potato, and various seeds, all of the same kind, from different soils and distant parts of England. He further states that with plants propagated by cuttings, as with the {147}
Pelargonium, and especially the Dahlia, manifest advantage is derived from getting plans of the same variety, which have been cultivated in another place; or, "where the extent of the place allows, to take cuttings from one description of soil to plant on another, so as to afford the change that seems so necessary to the well-being of the plants." He maintains that after a time an exchange of this nature is "forced on the grower, whether he be prepared for it or not." Similar remarks have been made by another excellent gardener, Mr. Fish, namely, that cuttings of the same variety of Calceolaria, which he obtained from a neighbour, "showed much greater vigour than some of his own that were treated in exactly the same manner," and he attributed this solely to his own plants having become "to a certain extent worn out or tired of their quarters." Something of this kind apparently occurs in grafting and budding fruit-trees; for, according to Mr. Abbey, grafts or buds generally take on a distinct variety or even species, or on a stock previously grafted, with greater facility than on stocks raised from seeds of the variety which is to be grafted; and he believes this cannot be altogether explained by the stocks in question being better adapted to the soil and climate of the place. It should, however, be added, that varieties grafted or budded on very distinct kinds, though they may take more readily and grow at first more vigorously than when grafted on closely allied stocks, afterwards often become unhealthy.

I have studied M. Tessier's careful and elaborate experiments,[328] made to disprove the common belief that good is derived from a change of seed; and he certainly shows that the same seed may with care be cultivated on the same farm (it is not stated whether on exactly the same soil) for ten consecutive years without loss. Another excellent observer, Colonel Le Couteur,[329] has come to the same conclusion; but then he expressly adds, if the same seed be used, "that which is grown on land manured from the mixen one year becomes seed for land prepared with lime, and that

again becomes seed for land dressed with ashes, then for land dressed with mixed manure, and so on." But this in effect is a systematic exchange of seed, within the limits of the same farm.

On the whole the belief, which has long been held by many skilful cultivators, that good follows from exchanging seed, tubers, &c., seems to be fairly well founded. Considering the small size of most seeds, it seems hardly credible that the advantage thus derived can be due to the seeds obtaining in one soil some chemical element deficient in the other soil. As plants after once germinating naturally become fixed to the same spot, it might have been anticipated that they would show the good effects of a change more plainly than animals, which continually wander about; and this apparently is the case. Life depending on, or consisting in, an incessant play of the most complex forces, it would appear that their action is in some way stimulated by slight changes in the circumstances to which each organism is exposed. All forces throughout nature, as Mr. Herbert Spencer[330] remarks, tend towards an equilibrium, and for the life of each being it is necessary that this tendency should be checked. If these views and the foregoing facts can be trusted, they probably throw light, on the one hand, on the good effects of crossing the breed, for the germ will be thus slightly modified or acted on by new forces; and on the other hand, on the evil effects of close interbreeding prolonged during many generations, during which the germ will be acted on by a male having almost identically the same constitution. {148}

Sterility from changed Conditions of Life.

I will now attempt to show that animals and plants, when removed from their natural conditions, are often rendered in some degree infertile or completely barren; and this occurs even when the conditions have not been greatly changed. This conclusion is not necessarily opposed to that at which we have just arrived, namely, that lesser changes of other kinds are advantageous to organic beings. Our present subject is of some importance, from having an intimate connexion with the causes of variability. Indirectly it perhaps bears on the sterility of species when crossed: for as, on the one hand, slight changes in the conditions of life are favourable to plants and animals, and the crossing of varieties adds to the size, vigour, and fertility of their offspring; so, on the other hand, certain other changes in the conditions of life cause sterility; and as this likewise ensues from crossing much-modified forms or species, we have a parallel and double series of facts, which apparently stand in close relation to each other.

It is notorious that many animals, though perfectly tamed, refuse to breed in captivity. Isidore Geoffroy St. Hilaire[331] consequently has drawn a broad distinction between tamed animals which will not breed under captivity, and truly domesticated animals which breed freely—generally more freely, as shown in the sixteenth chapter, than in a state of nature. It is possible and generally easy to tame most animals; but experience has shown that it is difficult to get them to breed regularly, or even at all. I shall discuss this subject in detail; but will give only those cases which seem most illustrative. My materials are derived from notices scattered through various works, and especially from a Report, drawn up for me by the kindness of the officers of the Zoological Society of London, which has especial value, as it records all the cases, during nine years from 1838-46, in which the animals were seen to couple but produced no offspring, as well as the cases in which they never, as far as known, coupled. This MS. Report I have corrected by the annual Reports subsequently published. Many facts are given on the breeding of the animals in that magnificent work, 'Gleanings from the Menageries of Knowsley Hall,' by Dr. Gray. I made, also, particular inquiries from the experienced keeper of the birds in the old Surrey Zoological Gardens. I should premise that a slight change in the treatment of animals sometimes makes a great difference in their fertility; and it is probable that the results observed in different menageries would differ. Indeed some animals in our Zoological Gardens have become {149}

more productive since the year 1846. It is, also, manifest from F. Cuvier's account of the Jardin des Plantes,[332] that the animals formerly bred much less freely there than with us; for instance, in the Duck tribe, which is highly prolific, only one species had at that period produced young.

The most remarkable cases, however, are afforded by animals kept in their native country, which, though perfectly tamed, quite healthy, and allowed some freedom, are absolutely incapable of breeding. Rengger,[333] who in Paraguay particularly attended to this subject, specifies six quadrupeds in this condition; and he mentions two or three others which most rarely breed. Mr. Bates, in his admirable work on the {150}
Amazons, strongly insists on similar cases;[334] and he remarks, that the fact of thoroughly tamed native mammals and birds not breeding when kept by the Indians, cannot be wholly accounted for by their negligence or indifference, for the turkey is valued by them, and the fowl has been adopted by the remotest tribes. In almost every part of the world—for instance, in the interior of Africa, and in several of the Polynesian islands—the natives are extremely fond of taming the indigenous quadrupeds and birds; but they rarely or never succeed in getting them to breed.

The most notorious case of an animal not breeding in captivity is that of the elephant. Elephants are kept in large numbers in their native Indian home, live to old age, and are vigorous enough for the severest labour; yet, with one or two exceptions, they have never been known even to couple, though both males and females have their proper periodical seasons. If, however, we proceed a little eastward to Ava, we hear from Mr. Crawfurd[335] that their "breeding in the domestic state, or at least in the half-domestic state in which the female elephants are generally kept, is of every-day occurrence;" and Mr. Crawfurd informs me that he believes that the difference must be attributed solely to the females being allowed to roam the forests with some degree of freedom. The captive rhinoceros, on the other hand, seems from Bishop Heber's account[336] to breed in India far more readily than the elephant. Four wild species of the horse genus have bred in Europe, though here exposed to a great change in their natural habits of life; but the species have generally been crossed one with another. Most of the members of the pig family breed readily in our menageries: even the Red River hog (*Potamochœrus penicillatus*), from the sweltering plains of West Africa, has bred twice in the Zoological Gardens. Here also the Peccary (*Dicotyles torquatus*) has bred several times; but another species, the *D. labiatus*, though rendered so tame as to be half-domesticated, breeds so rarely in its native country of Paraguay, that according to Rengger[337] the fact requires confirmation. Mr. Bates remarks that the tapir, though often kept tame in Amazonia by the Indians, never breeds.

Ruminants generally breed quite freely in England, though brought from widely different climates, as may be seen in the Annual Reports of the Zoological Gardens, and in the Gleanings from Lord Derby's menagerie.

The Carnivora, with the exception of the Plantigrade division, generally breed (though with capricious exceptions) almost as freely as ruminants. Many species of Felidæ have bred in various menageries, although imported from various climates and closely confined. Mr. Bartlett, the present superintendent of the Zoological Gardens,[338] remarks that the lion appears to breed more frequently and to bring forth more young at a birth than any other species of the family. He adds that the tiger has rarely bred; "but there are several well-authenticated instances of the female tiger breeding with {151}
the lion." Strange as the fact may appear, many animals under confinement unite with distinct species and produce hybrids quite as freely as, or even more freely than, with their own species. On inquiring from Dr. Falconer and others, it appears that the tiger when confined in India does not breed, though it has been known to couple. The

cheetah (*Felis jubata*) has never been known by Mr. Bartlett to breed in England, but it has bred at Frankfort; nor does it breed in India, where it is kept in large numbers for hunting; but no pains would be taken to make them breed, as only those animals which have hunted for themselves in a state of nature are serviceable and worth training.[339] According to Rengger, two species of wild cats in Paraguay, though thoroughly tamed, have never bred. Although so many of the Felidæ breed readily in the Zoological Gardens, yet conception by no means always follows union: in the nine-year Report, various species are specified which were observed to couple seventy-three times, and no doubt this must have passed many times unnoticed; yet from the seventy-three unions only fifteen births ensued. The Carnivora in the Zoological Gardens were formerly less freely exposed to the air and cold than at present, and this change of treatment, as I was assured by the former superintendent, Mr. Miller, greatly increased their fertility. Mr. Bartlett, and there cannot be a more capable judge, says, "it is remarkable that lions breed more freely in travelling collections than in the Zoological Gardens; probably the constant excitement and irritation produced by moving from place to place, or change of air, may have considerable influence in the matter."

Many members of the Dog family breed readily when confined. The Dhole is one of the most untameable animals in India, yet a pair kept there by Dr. Falconer produced young. Foxes, on the other hand, rarely breed, and I have never heard of such an occurrence with the European fox: the silver fox of North America (*Canis argentatus*), however, has bred several times in the Zoological Gardens. Even the otter has bred there. Every one knows how readily the semi-domesticated ferret breeds, though shut up in miserably small cages; but other species of Viverra and Paradoxurus absolutely refuse to breed in the Zoological Gardens. The Genetta has bred both here and in the Jardin des Plantes, and produced hybrids. The *Herpestes fasciatus* has likewise bred; but I was formerly assured that the *H. griseus*, though many were kept in the Gardens, never bred.

The Plantigrade Carnivora breed under confinement much less freely, without our being able to assign any reason, than other members of the group. In the nine-year Report it is stated that the bears had been seen in the Zoological Gardens to couple freely, but previously to 1848 had most rarely conceived. In the Reports published since this date three species have produced young (hybrids in one case), and, wonderful to relate, the white Polar bear has produced young. The badger (*Meles taxus*) has bred several times in the Gardens; but I have not heard of this occurring {152} elsewhere in England, and the event must be very rare, for an instance in Germany has been thought worth recording.[340] In Paraguay the native Nasua, though kept in pairs during many years and perfectly tamed, has never been known, according to Rengger, to breed or show any sexual passion; nor, as I hear from Mr. Bates, does this animal, or the Cercoleptes, breed in the region of the Amazons. Two other plantigrade genera, Procyon and Gulo, though often kept tame in Paraguay, never breed there. In the Zoological Gardens species of Nasua and Procyon have been seen to couple; but they did not produce young.

As domesticated rabbits, guinea-pigs, and white mice breed so abundantly when closely confined under various climates, it might have been thought that most other members of the Rodent order would have bred in captivity, but this is not the case. It deserves notice, as showing how the capacity to breed sometimes goes by affinity, that the one native rodent of Paraguay, which there breeds *freely* and has yielded successive generations, is the *Cavia aperea*; and this animal is so closely allied to the guinea-pig, that it has been erroneously thought to be the parent-form.[341] In the Zoological Gardens, some rodents have coupled, but have never produced young;

some have neither coupled nor bred; but a few have bred, as the porcupine more than once, the Barbary mouse, lemming, chinchilla, and the agouti (*Dasyprocta aguti*), several times. This latter animal has also produced young in Paraguay, though they were born dead and ill-formed; but in Amazonia, according to Mr. Bates, it never breeds, though often kept tame about the houses. Nor does the paca (*Cœlogenys paca*) breed there. The common hare when confined has, I believe, never bred in Europe; [342] though, according to a recent statement, it has crossed with the rabbit. I have never heard of the dormouse breeding in confinement. But squirrels offer a more curious case: with one exception, no species has ever bred in the Zoological Gardens, yet as many as fourteen individuals of *S. palmarum* were kept together during several years. The *S. cinerea* has been seen to couple, but it did not produce young; nor has this species, when rendered extremely tame in its native country, North America, been ever known to breed.[343] At Lord Derby's menagerie squirrels of many kinds were kept in numbers, but Mr. Thompson, the superintendent, told me that none had ever bred there, or elsewhere as far as he knew. I have never heard of the English squirrel breeding in confinement. But the species which has bred more than once in the Zoological Gardens is the one which perhaps might have been least expected, namely, the flying squirrel (*Sciuropterus volucella*): it has, also, bred several times near {153}
Birmingham; but the female never produced more than two young at a birth, whereas in its native American home she bears from three to six young.[344]

Monkeys, in the nine-year Report from the Zoological Gardens, are stated to unite most freely, but during this period, though many individuals were kept, there were only seven births. I have heard of one American monkey alone, the Ouistiti, breeding in Europe.[345] A Macacus, according to Flourens, bred in Paris; and more than one species of this genus has produced young in London, especially the *Macacus rhesus*, which everywhere shows a special capacity to breed under confinement. Hybrids have been produced both in Paris and London from this same genus. The Arabian baboon, or *Cynocephalus hamadryas*,[346] and a Cercopithecus have bred in the Zoological Gardens, and the latter species at the Duke of Northumberland's. Several members of the family of Lemurs have produced hybrids in the Zoological Gardens. It is much more remarkable that monkeys very rarely breed when confined in their native country; thus the Cay (*Cebus azaræ*) is frequently and completely tamed in Paraguay, but Rengger[347] says that it breeds so rarely, that he never saw more than two females which had produced young. A similar observation has been made with respect to the monkeys which are frequently tamed by the aborigines in Brazil.[348] In the region of the Amazons, these animals are so often kept in a tame state, that Mr. Bates in walking through the streets of Parà counted thirteen species; but, as he asserts, they have never been known to breed in captivity.[349]

Birds.

Birds offer in some respects better evidence than quadrupeds, from their breeding more rapidly and being kept in greater numbers. We have seen that carnivorous animals are more fertile under confinement than most other mammals. The reverse holds good with carnivorous birds. It is said[350] that as many as eighteen species have been used in Europe for hawking, and several others in Persia and India;[351] they have been kept in their native country in the finest condition, and have been flown during six, eight, or nine years;[352] yet there is no record of their having ever produced young. As these birds were formerly caught whilst young, at great expense, being imported from Iceland, Norway, and Sweden, there can be little doubt that, if {154}
possible, they would have been propagated. In the Jardin des Plantes, no bird of prey

has been known to couple.[353] No hawk, vulture, or owl has ever produced fertile eggs in the Zoological Gardens, or in the old Surrey Gardens, with the exception, in the former place on one occasion, of a condor and a kite (*Milvus niger*). Yet several species, namely, the *Aquila fusca*, *Haliætus leucocephalus*, *Falco tinnunculus*, *F. subbuteo*, and *Buteo vulgaris*, have been seen to couple in the Zoological Gardens. Mr. Morris[354] mentions as a unique fact that a kestrel (*Falco tinnunculus*) bred in an aviary. The one kind of owl which has been known to couple in the Zoological Gardens was the Eagle Owl (*Bubo maximus*); and this species shows a special inclination to breed in captivity; for a pair at Arundel Castle, kept more nearly in a state of nature "than ever fell to the lot of an animal deprived of its liberty,"[355] actually reared their young. Mr. Gurney has given another instance of this same owl breeding in confinement; and he records the case of a second species of owl, the *Strix passerina*, breeding in captivity.[356]

Of the smaller graminivorous birds, many kinds have been kept tame in their native countries, and have lived long; yet, as the highest authority on cage-birds[357] remarks, their propagation is "uncommonly difficult." The canary-bird shows that there is no inherent difficulty in these birds breeding freely in confinement; and Audubon says[358] that the *Fringilla* (*Spiza*) *ciris* of North America breeds as perfectly as the canary. The difficulty with the many finches which have been kept in confinement is all the more remarkable as more than a dozen species could be named which have yielded hybrids with the canary; but hardly any of these, with the exception of the siskin (*Fringilla spinus*), have reproduced their own kind. Even the bullfinch (*Loxia pyrrhula*) has bred as frequently with the canary, though belonging to a distinct genus, as with its own species.[359] With respect to the skylark (*Alauda arvensis*), I have heard of birds living for seven years in an aviary, which never produced young; and a great London bird-fancier assured me that he had never known an instance of their breeding; nevertheless one case has been recorded.[360] In the nine-year Report from the Zoological Society, twenty-four incessorial species are enumerated which had not bred, and of these only four were known to have coupled.

Parrots are singularly long-lived birds; and Humboldt mentions the curious fact of a parrot in South America, which spoke the language of an extinct Indian tribe, so that this bird preserved the sole relic of a lost language. Even in this country there is reason to believe[361] that parrots have lived to the age of nearly one hundred years; yet, though many have been kept in Europe, they breed so rarely that the event has been thought worth recording in the gravest publications.[362] According to Bechstein[363] the African *Psittacus erithacus* breeds oftener than any other species: the *P. macoa* occasionally lays fertile eggs, but rarely succeeds in hatching them; this bird, however, has the instinct of incubation sometimes so strongly developed, that it will hatch the eggs of fowls or pigeons. In the Zoological Gardens and in the old Surrey Gardens some few species have coupled, but, with the exception of three species of parrakeets, none have bred. It is a much more remarkable fact that in Guiana parrots of two kinds, as I am informed by Sir E. Schomburgk, are often taken from the nests by the Indians and reared in large numbers; they are so tame that they fly freely about the houses, and come when called to be fed, like pigeons; yet he has never heard of a single instance of their breeding.[364] In Jamaica, a resident naturalist, Mr. R. Hill,[365] says, "no birds more readily submit to human dependence than the parrot-tribe, but no instance of a parrot breeding in this tame life has been known yet." Mr. Hill specifies a number of other native birds kept tame in the West Indies, which never breed in this state.

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The great pigeon family offers a striking contrast with parrots: in the nine-year Report thirteen species are recorded as having bred, and, what is more noticeable, only two were seen to couple without any result. Since the above date every annual Report gives many cases of various pigeons breeding. The two magnificent crowned pigeons (*Goura coronata* and *Victoriæ*) produced hybrids; nevertheless, of the former species more than a dozen birds were kept, as I am informed by Mr. Crawfurd, in a park at Penang, under a perfectly well-adapted climate, but never once bred. The *Columba migratoria* in its native country, North America, invariably lays two eggs, but in Lord Derby's menagerie never more than one. The same fact has been observed with the *C. leucocephala*.[366]

Gallinaceous birds of many genera likewise show an eminent capacity for breeding under captivity. This is particularly the case with pheasants; yet our English species seldom lays more than ten eggs in confinement; whilst from eighteen to twenty is the usual number in the wild state.[367] With the Gallinaceæ, as with all other orders, there are marked and inexplicable exceptions in regard to the fertility of certain species and {156}
genera under confinement. Although many trials have been made with the common partridge, it has rarely bred, even when reared in large aviaries; and the hen will never hatch her own eggs.[368] The American tribe of Guans or Cracidæ are tamed with remarkable ease, but are very shy breeders in this country;[369] but with care various species were formerly made to breed rather freely in Holland.[370] Birds of this tribe are often kept in a perfectly tamed condition in their native country by the Indians, but they never breed.[371] It might have been expected that grouse from their habits of life would not have bred in captivity, more especially as they are said soon to languish and die.[372] But many cases are recorded of their breeding: the capercailzie (*Tetrao urogallus*) has bred in the Zoological Gardens; it breeds without much difficulty when confined in Norway, and in Russia five successive generations have been reared: *Tetrao tetrix* has likewise bred in Norway; *T. Scoticus* in Ireland; *T. umbellus* at Lord Derby's; and *T. cupido* in North America.

It is scarcely possible to imagine a greater change in habits than that which the members of the ostrich family must suffer, when cooped up in small enclosures under a temperate climate, after freely roaming over desert and tropical plains or entangled forests. Yet almost all the kinds, even the mooruk (*Casuarius Bennettii*) from New Ireland, has frequently produced young in the various European menageries. The African ostrich, though perfectly healthy and living long in the South of France, never lays more than from twelve to fifteen eggs, though in its native country it lays from twenty-five to thirty.[373] Here we have another instance of fertility impaired, but not lost, under confinement, as with the flying squirrel, the hen-pheasant, and two species of American pigeons.

Most Waders can be tamed, as the Rev. E. S. Dixon informs me, with remarkable facility; but several of them are short-lived under confinement, so that their sterility in this state is not surprising. The cranes breed more readily than other genera: *Grus montigresia* has bred several times in Paris and in the Zoological Gardens, as has *G. cinerea* at the latter place, and *G. antigone* at Calcutta. Of other members of this great order, *Tetrapteryx paradisea* has bred at Knowsley, a Porphyrio in Sicily, and the *Gallinula chloropus* in the Zoological Gardens. On the other hand, several birds {157}
belonging to this order will not breed in their native country, Jamaica; and the Psophia, though often kept by the Indians of Guiana about their houses, "is seldom or never known to breed."[374]

No birds breed with such complete facility under confinement as the members of the great Duck family; yet, considering their aquatic and wandering habits, and the nature of their food, this could not have been anticipated. Even some time ago above two dozen species had bred in the Zoological Gardens; and M. Selys-Longchamps has recorded the production of hybrids from forty-four different members of the family; and to these Professor Newton has added a few more cases.[375] "There is not," says Mr. Dixon,[376] "in the wide world, a goose which is not in the strict sense of the word domesticable;" that is, capable of breeding under confinement; but this statement is probably too bold. The capacity to breed sometimes varies in individuals of the same species; thus Audubon[377] kept for more than eight years some wild geese (*Anser Canadensis*), but they would not mate; whilst other individuals of the same species produced young during the second year. I know of but one instance in the whole family of a species which absolutely refuses to breed in captivity, namely, the *Dendrocygna viduata*, although, according to Sir R. Schomburgk,[378] it is easily tamed, and is frequently kept by the Indians of Guiana. Lastly, with respect to Gulls, though many have been kept in the Zoological Gardens and in the old Surrey Gardens, no instance was known before the year 1848 of their coupling or breeding; but since that period the herring gull (*Larus argentatus*) has bred many times in the Zoological Gardens and at Knowsley.

There is reason to believe that insects are affected by confinement like the higher animals. It is well known that the Sphingidæ rarely breed when thus treated. An entomologist[379] in Paris kept twenty-five specimens of *Saturnia pyri*, but did not succeed in getting a single fertile egg. A number of females of *Orthosia munda* and of *Mamestra suasa* reared in confinement were unattractive to the males.[380] Mr. Newport kept nearly a hundred individuals of two species of Vanessa, but not one paired; this, however, might have been due to their habit of coupling on the wing.[381] Mr. Atkinson could never succeed in India in making the Tarroo silk-moth breed in confinement.[382] It appears that a number of moths, especially the Sphingidæ, when hatched in the autumn out of their proper season, are completely barren; but this latter case is still involved in some obscurity.[383] {158}

Independently of the fact of many animals under confinement not coupling, or, if they couple, not producing young, there is evidence of another kind, that their sexual functions are thus disturbed. For many cases have been recorded of the loss by male birds when confined of their characteristic plumage. Thus the common linnet (*Linota cannabina*) when caged does not acquire the fine crimson colour on its breast, and one of the buntings (*Emberiza passerina*) loses the black on its head. A Pyrrhula and an Oriolus have been observed to assume the quiet plumage of the hen-bird; and the *Falco albidus* returned to the dress of an earlier age.[384] Mr. Thomson, the superintendent of the Knowsley menagerie, informed me that he had often observed analogous facts. The horns of a male deer (*Cervus Canadensis*) during the voyage from America were badly developed; but subsequently in Paris perfect horns were produced.

When conception takes place under confinement, the young are often born dead, or die soon, or are ill-formed. This frequently occurs in the Zoological Gardens, and, according to Rengger, with native animals confined in Paraguay. The mother's milk often fails. We may also attribute to the disturbance of the sexual functions the frequent occurrence of that monstrous instinct which leads the mother to devour her own offspring,—a mysterious case of perversion, as it at first appears.

Sufficient evidence has now been advanced to prove that animals when first confined are eminently liable to suffer in their reproductive systems. We feel at first naturally inclined to

attribute the result to loss of health, or at least to loss of vigour; but this view can hardly be admitted when we reflect how healthy, long-lived, and vigorous many animals are under captivity, such as parrots, and hawks when used for hawking, chetahs when used for {159} hunting, and elephants. The reproductive organs themselves are not diseased; and the diseases, from which animals in menageries usually perish, are not those which in any way affect their fertility. No domestic animal is more subject too disease than the sheep, yet it is remarkably prolific. The failure of animals to breed under confinement has been sometimes attributed exclusively to a failure in their sexual instincts: this may occasionally come into play, but there is no obvious reason why this instinct should be especially liable to be affected with perfectly tamed animals, except indeed indirectly through the reproductive system itself being disturbed. Moreover, numerous cases have been given of various animals which couple freely under confinement, but never conceive; or, if they conceive and produce young, these are fewer in number than is natural to the species. In the vegetable kingdom instinct of course can play no part; and we shall presently see that plants when removed from their natural conditions are affected in nearly the same manner as animals. Change of climate cannot be the cause of the loss of fertility, for, whilst many animals imported into Europe from extremely different climates breed freely, many others when confined in their native land are completely sterile. Change of food cannot be the chief cause; for ostriches, ducks, and many other animals, which must have undergone a great change in this respect, breed freely. Carnivorous birds when confined are extremely sterile; whilst most carnivorous mammals, except plantigrades, are moderately fertile. Nor can the amount of food be the cause; for a sufficient supply will certainly be given to valuable animals; and there is no reason to suppose that much more food would be given to them, than to our choice domestic productions which retain their full fertility. Lastly, we may infer from the case of the elephant, chetah, various hawks, and of many animals which are allowed to lead an almost free life in their native land, that want of exercise is not the sole cause.

It would appear that any change in the habits of life, whatever these habits may be, if great enough, tends to affect in an inexplicable manner the powers of reproduction. The result depends more on the constitution of the species than on the nature of the change; for certain {160} whole groups are affected more than others; but exceptions always occur, for some species in the most fertile groups refuse to breed, and some in the most sterile groups breed freely. Those animals which usually breed freely under confinement, rarely breed, as I was assured, in the Zoological Gardens, within a year or two after their first importation. When an animal which is generally sterile under confinement happens to breed, the young apparently do not inherit this power; for had this been the case, various quadrupeds and birds, which are valuable for exhibition, would have become common. Dr. Broca even affirms[385] that many animals in the Jardin des Plantes, after having produced young for three or four successive generations, become sterile; but this may be the result of too close interbreeding. It is a remarkable circumstance that many mammals and birds have produced hybrids under confinement quite as readily as, or even more readily than, they have procreated their own kind. Of this fact many instances have been given;[386] and we are thus reminded of those plants which when cultivated refuse to be fertilised by their own pollen, but can easily be fertilised by that of a distinct species. Finally, we must conclude, limited as the conclusion is, that changed conditions of life have an especial power of acting injuriously on the reproductive system. The whole case is quite peculiar, for these organs, though not diseased, are thus rendered incapable of performing their proper functions, or perform them imperfectly.

Sterility of Domesticated Animals from changed conditions.—With respect to domesticated animals, as their domestication mainly depends on the accident of their breeding freely under captivity, we ought not to expect that their reproductive system would be affected by any moderate degree of change. Those orders of quadrupeds and

birds, of which the wild species breed most readily in our menageries, have afforded us the greatest number of domesticated productions. Savages in most parts of the world are fond of taming animals;[387] and if any of these regularly produced young, {161} and were at the same time useful, they would be at once domesticated. If, when their masters migrated into other countries, they were in addition found capable of withstanding various climates, they would be still more valuable; and it appears that the animals which breed readily in captivity can generally withstand different climates. Some few domesticated animals, such as the reindeer and camel, offer an exception to this rule. Many of our domesticated animals can bear with undiminished fertility the most unnatural conditions; for instance, rabbits, guinea-pigs, and ferrets breed in miserably confined hutches. Few European dogs of any kind withstand without degeneration the climate of India; but as long as they survive, they retain, as I hear from Mr. Falconer, their fertility; so it is, according to Dr. Daniell, with English dogs taken to Sierra Leone. The fowl, a native of the hot jungles of India, becomes more fertile than its parent-stock in every quarter of the world, until we advance as far north as Greenland and Northern Siberia, where this bird will not breed. Both fowls and pigeons, which I received during the autumn direct from Sierra Leone, were at once ready to couple.[388] I have, also, seen pigeons breeding as freely as the common kinds within a year after their importation from the Upper Nile. The guinea-fowl, an aboriginal of the hot and dry deserts of Africa, whilst living under our damp and cool climate, produces a large supply of eggs.

Nevertheless, our domesticated animals under new conditions occasionally show signs of lessened fertility. Roulin asserts that in the hot valleys of the equatorial Cordillera sheep are not fully fecund;[389] and according to Lord Somerville,[390] the merino-sheep which he imported from Spain were not at first perfectly fertile. It is said[391] that mares brought up on dry food in the stable, and turned out to grass, do not at first breed. The peahen, as we have seen, is said not to lay so many eggs in England as in India. It was long before the canary-bird was fully fertile, and even now first-rate breeding birds are not common.[392] In the hot and dry province of Delhi, the eggs of the turkey, as I hear from Dr. Falconer, though placed under a hen, are extremely liable to fail. According to Roulin, geese taken within a recent period to the lofty plateau of Bogota, at first laid seldom, and then only a few eggs; of these scarcely a fourth were hatched, and half the young birds died: in the second generation they were more fertile; and when Roulin wrote they were becoming as fertile as our geese in Europe. In the Philippine Archipelago the goose, it is asserted, {162} will not breed or even lay eggs.[393] A more curious case is that of th