# VARIATION OF ANIMALS AND PLANTS

#### UNDER DOMESTICATION.

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## CHAPTER XIII.

#### 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 *Rückschlag*, or *Rückschritt*. 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 in the last case we must attribute this 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 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 as the mother cannot possess or exhibit such male attributes, the child must inherit 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 one another; 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 an individual with some distinguishable character, a race, or species, has at some former period been crossed, 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 breeds of the pigeon, of blue birds with all the marks characteristic of the wild Columba livia. Similar

cases were given in the case of the fowl. With the common ass, as the legs of the wild progenitor are almost always 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 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 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."<sup>1</sup> 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 produced.<sup>2</sup>

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.<sup>3</sup> At the present day, notwithstanding the great care which is taken to prevent it, particoloured lambs and some entirely black are occasionally, or even frequently, 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 blackspotted, or wholly black lambs appear.<sup>4</sup> This occurs still more frequently with the less improved breeds, such as the Norfolks.<sup>5</sup> As bearing on this tendency in sheep to revert to dark colours, I may state (though in doing so I trench on

<sup>1</sup> Youatt on Sheep, pp. 20, 234. The same fact of loose horns occasionally appearing in hornless breeds has been observed in Germany; Bechstein, 'Naturgesch. Deutschlands,' b. i. s. 362.

- <sup>2</sup> Youatt on Cattle, pp. 155, 174.
- <sup>9</sup> Youatt on Sheep, 1838, pp. 17,

145.

<sup>4</sup> I have been informed of this fact through the Rev. W. D. Fox, on the excellent authority of Mr. Wilmot: *see*, also, remarks on this subject in an article in the 'Quarterly Review,' 1849, p. 395.

<sup>5</sup> Youatt, pp. 19, 234.

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 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 breeeds of various animals. For instance, Mr. Hewitt<sup>6</sup> 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;"<sup>7</sup> 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

<sup>6</sup> 'The Poultry Book,' by Mr. Tegetmeier, 1866, p. 231. <sup>7</sup> Loudon's 'Gard. Mag.,' vol. x.,

<sup>7</sup> Loudon's 'Gard. Mag.,' vol. x., 1834, p. 396: a nurseryman, with much experience on this subject, has likewise assured me that this sometimes occurs.

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<sup>8</sup> and carrot-beds a few plants often "break"-that is, flower too soon ; and their roots are generally 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;<sup>9</sup> 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."

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.<sup>10</sup> In several cases we do not know the aboriginal parent-species, and cannot possibly tell

<sup>8</sup> 'Gardener's Chron.,' 1855, p. 777.

<sup>9</sup> Ibid., 1862, p. 721.

<sup>10</sup> Mr. Boner speaks ('Chamois-hunting,' 2nd edit., 1860, p. 92) of sheep often running wild in the Bavarian Alps; but, on making further inquiries at my request, he

found that they are not able to establish themselves; they generally perish from the frozen snow clinging to their wool, and they have lost the skill necessary to pass over steep icy slopes. On one occasion two ewes survived the winter, but their lambs perished.

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<sup>11</sup> 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; if thus destroyed, they would 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

<sup>11</sup> See some excellent remarks on Proc. Linn. Soc.,' 1858, vol. iii. p. 60. this subject by Mr. Wallace, 'Journal

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 several respects. In Louisiana the pig<sup>12</sup> 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,<sup>13</sup> 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<sup>14</sup> has strongly insisted on what slight evidence the common belief in their reversion to a primitive state rests. Godron<sup>15</sup> 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,—characters which would certainly be lost by plants growing in 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 the wild Mediterranean species, which is said not to be social (though this may be due merely to the nature of the conditions), 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 recognisable 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 expres-

<sup>12</sup> Dureau de la Malle, in 'Comptes Rendus,' tom. xli., 1855, p. 807. From the statements above given, the author concludes that the wild pigs of Louisiana are not descended from the European Sus scrofa.

<sup>13</sup> Capt. W. Allen, in his 'Expedition to the Niger,' states that fowls have run wild on the island of Annobon, and have become modified in form and voice. The account is so meagre and vague that it did not appear to me worth copying; but I now find that Dureau de la Malle ('Comptes Rendus,' tom. xli., 1855, p. 690) advances this as a good instance of reversion to the primitive stock, and as confirmatory of a still more vague statement in classical times by Varro.

<sup>14</sup> 'Flora of Australia,' 1859, Introduct., p. ix.

<sup>13</sup> 'De l'Espèce,' tom. ii. pp. 54, 58, 60.

sion, one of their grandparents, or some more distant collateral relation. Very many anomalies of structure and diseases,<sup>16</sup> 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 I may give one other instance, on the authority of veins. Mr. R. Walker, a large cattle-breeder in Kincardineshire. He bought a black bull, the son of a black cow with white legs, white belly and part of the tail white; and in 1870 a calf the gr.-gr.-gr.-grandchild of this cow was born coloured in the same very peculiar manner; all the intermediate offspring having been black. In these cases there can hardly be a doubt that a character derived from a cross with an individual of the same variety reappeared after passing over three generations in the one case, and five in the other.

When two distinct races are crossed, it is notorious that the tendency in the offspring to revert to one or both parentforms 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<sup>17</sup> 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

<sup>16</sup> Mr. Sedgwick gives many in-stances in the 'British and Foreign Med.-Chirurg. Review,' April and

July, 1863, pp. 448, 188. <sup>17</sup> In his edit. of 'Youatt on the Pig,' 1860, p. 27.

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.<sup>18</sup> 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 which were gained by a cross, with those 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 as powerful with hybrids, when they are sufficiently fertile to breed together, or when they are repeatedly crossed with either pure parent-form, as in the case of mongrels. It is not necessary to give instances. With 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 ones than

<sup>18</sup> Dr. P. Lucas, 'Héréd. Nat.,' tom. ii. pp. 314, 892: see a good practical article on the subject in 'Gard. Chronicle,' 1856, p. 620. I could add a vast number of references, but they would be superfluous.

Naudin.<sup>19</sup> The tendency differs in degree or strength in different groups, and partly depends, as we shall presently see, on whether the parent-plants have 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; it may also 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 reappearing 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. Sometimes 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."<sup>20</sup>

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, a 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, reassume their former character; and here we have reversion

20 Quoted by Mr. Sedgwick in

'Med.-Chirurg. Review,' April, 1861, p. 485. Dr. H. Dobell, in 'Med.-Chirurg. Transactions,' vol. xlvi., gives an analogous case, in which, in a large family, fingers with thickened joints were transmitted to several members during five generations; but when the blemish once disappeared it never reappeared.

<sup>&</sup>lt;sup>19</sup> Kölreuter gives curious cases in his 'Dritte Fortsetzung,' 1766, ss. 53, 59; and in his well-known 'Memoirs on Lavatera and Jalapa.' Gärtner, 'Bastarderzeugung,' ss. 437, 441, &c. Naudin, in his "Recherches sur P'Hybridité," 'Nouvelles Archives du Muséum,' tom. i. p. 25.

by segments. Vilmorin<sup>21</sup> 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.

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<sup>22</sup> insists in his discussion on disjunction of character, are closely analogous with those given in the eleventh chapter. in which crossed plants have been known to produce halfand-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, 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 budgenerations on the same plant, they may be thus included.

Analogous facts have been observed in the animal kingdom, <sup>21</sup> Verlot, 'Des Variétés,' 1865, p. 63.

<sup>22</sup> 'Nouvelles Archives du Muséum,'

tom. i. p. 25. Alex. Braun (in his 'Rejuvenescence,' Ray Soc., 1853, p. 315) apparent<sup>1</sup>y holds a similar opinion.

and are more remarkable, as they occur in the same individual in the strictest sense, 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 <sup>23</sup> 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 at first showed not a trace of the frill, but, after moulting thrice, a small yet unmistakably distinct frill appeared on its breast. According to Girou,<sup>24</sup> 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. possess a dog, the daughter of a white terrier by a foxcoloured bulldog; as a puppy she was quite white, but when about six months old a black spot appeared on her nose, and brown spots on her ears. When a little older she was badly wounded on the back, and the hair which grew on the cicatrix was of a brown colour, apparently derived from her father. This is the more remarkable, as with most animals having coloured hair, that which grows on a wounded surface is white.

In the foregoing cases, the characters which with advancing age reappeared, were present in the immediately preceding

<sup>22</sup> Mr. Teebay, in 'The Poultry 2<sup>4</sup> Quoted by Hofacker, 'Ueber die Book,' by Mr. Tegetmeier, 1866, p. Eigenschaften,' &c., s. 98.
 72.

generations; but characters sometimes reappear in the same manner after a much longer interval of time. Thus 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.<sup>25</sup> 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."<sup>26</sup> 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.<sup>27</sup> Now as Gallus bankiva is coloured red and orange, and as Dorking fowls and 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

<sup>25</sup> Azara, 'Essais Hist. Nat. de Paraguay,' tom. ii. 1801, p. 372.
<sup>26</sup> These facts are given on the high authority of Mr. Hewitt, in

'The Poultry Book,' by Mr. Teget-

meier, 1866, p. 248. 27 'The Poultry Book,' by Tegetmeier, 1866, p. 97.

conclusion seems to me highly 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 of pigeons, birds 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 often 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 excellent observer the opportunity of inspecting some neck-hackles and tailfeathers 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 fluxk-duck (*Cairina 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. I hear from Mr. Blyth that hybrids from the canary and gold-finch almost always have streaked feathers on their backs; and this streaking must be derived from the original wild canary.

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 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 it 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 guite wild in two distant parts of the world, are likewise thus coloured. Now, an experienced breeder, Mr. J. Beasley, of Northamptonshire,<sup>28</sup> 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 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<sup>29</sup> 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

<sup>29</sup> Ibid., 1860, p. 343. I am glad to find that so experienced a breeder of cattle as Mr. Willoughby Wood ('Gard. Chron.' 1869, p. 1216), admits my principle of a cross giving a tendency to reversion.

<sup>&</sup>lt;sup>28</sup> 'Gardener's Chron. and Agricultural Gazette,' 1866, p. 528.

In foals they are sometimes plainly seen, and kinds of duns. 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 considered as a reversion to the wild parent form, the Equus taniopus of Abyssinia,<sup>30</sup> which is generally 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 more frequently 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 fallowduns. 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,<sup>31</sup> and remarks that mules are particularly liable to be thus striped on their legs. In South America, according to Roulin,<sup>32</sup> such stripes are more frequent and conspicuous in the mule than in the ass. In the United States, Mr. Gosse,<sup>33</sup> 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 shoulderstripes, 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 a conspicuously striped body and 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,<sup>34</sup> that the legs are much more conspicuously striped than the rest of the body; and this fact is intelligible only on the belief

<sup>30</sup> Sclater, in 'Proc. Zoolog. Soc.,' 1862, p. 163.

<sup>31</sup> 'History of the Horse,' p. 212.

<sup>32</sup> 'Mém. présentés par divers Savans à l'Acad. Royale,' tom. vi.

1835, p. 338. <sup>33</sup> 'Letters from Alabama,' 1859, p. 280.

34 'Hist. Nat. des Mammifères,' 1820, tom. i.

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,<sup>35</sup> from a chestnut, 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 Equus indicus<sup>36</sup> 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;<sup>37</sup> 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<sup>38</sup> 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.

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 parent-form 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 my experiments on crossed pigeons and fowls, will come to the same conclusion with respect to the horse-genus; and if so, 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.

Lastly, Professor Jaeger has given<sup>39</sup> a good case with pigs. He

<sup>35</sup> 'Philosoph. Transact.,' 1821, p. 20.

<sup>36</sup> Sclater, in 'Proc. Zoolog. Soc.,' 1862, p. 163: this species is the Ghor-Khur of N.W. India, and has often been called the Hemionus of Pallas. *See*, also, Mr. Blyth's excellent paper in 'Journal of Asiatic Soc. of Bengal,' vol. xxviii., 1860, p. 229.

<sup>37</sup> Another species of wild ass, the true *E. hemionus* or *Kiang*, which ordinarily has no shoulder-stripes, is said occasionally to have them; and these, as with the horse and ass, are sometimes double: see Mr. Blyth, in the paper just quoted, and in 'Indian Sporting Review,' 1856, p. 320: and Col. Hamilton Smith, in 'Nat. Library, Horses,' p. 318; and 'Dict. Class. d'Hist. Nat.,' tom. iii. p. 563. <sup>38</sup> Figured in the 'Gleanings from

<sup>38</sup> Figured in the 'Gleanings from the Knowsley Menageries,' by Dr. J. E. Gray.

<sup>39</sup> 'Ďarwin'sche Theorie und ihre Stellung zu Moral und Religion,' p. 85. crossed the Japanese or masked breed with the common German breed, and the offspring were intermediate in character. He then re-crossed one of these mongrels with the pure Japanese, and in the litter thus produced one of the young resembled in all its characters a wild pig; it had a long snout and upright ears, and was striped on the back. It should be borne in mind that the young of the Japanese breed are not striped, and that they have a short muzzle and ears remarkably dependent.

A similar tendency to the recovery of long lost characters holds good even with the instincts of crossed animals. 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.<sup>40</sup> Yet the aboriginal species was of course a good incubator; and 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-sitting varieties almost invariably produces a mongrel that becomes broody, and sits with remarkable steadiness." 41 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

<sup>40</sup> Cases of both Spanish and Polish hens sitting are given in the 'Poultry Chronicle,' 1855, vol. iii. p. 477.

Chronicle,' 1855, vol. iii. p. 477. <sup>41</sup> 'The Poultry Book,' by Mr. Tegetmeier, 1866, pp. 119, 163. The author, who remarks on the two negatives ('Journ. of Hort.,' 1862, p. 325), states that two broods were raised from a Spanish cock and Silverpencilled Hamburg hen, neither of which are incubators, and no less than seven out of eight hens in these two broods "showed a perfect obstinacy in sitting." The Rev. E. S. Dixon ('Ornamental Poultry,' 1848, p. 200) says that chickens reared from a cross between Golden and Black Polish fowls, are "good and steady birds to sit." Mr. B. P. Brent informs me that he raised some good sitting hens by crossing Pencilled Hamburg and Polish breeds. A cross-bred bird from a Spanish nonincubating cock and Cochin incubating hen is mentioned in the 'Poultry Chronicle,' vol. iii. p. 13, as an "exemplary mother." On the other hand, an exceptional case is given in the 'Cottage Gardener,' 1860, p. 388, of a hen raised from a Spanish cock and black Polish hen which did not incubate.

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. Thus 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 showed any tendency to sit; but one of them 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 reappearance 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 both 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 a tamed animal, the hybrids are often wild to such a degree, that the fact is intelligible only on the principle that the cross has caused a partial return to a primitive disposition. Thus, 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 crossbred 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." Captain Hutton, in India, crossed a tame goat with a wild one from the Himalaya, and he remarked to me how surprisingly wild the offspring were. 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;" 42 but I have myself seen one exception to this rule. Mr. S. J. Salter,43

<sup>42</sup> 'The Poultry Book,' by Tegetmeier, 1866, pp. 165, 167. <sup>43</sup> 'Natural History Review,' 1863, April, p. 277. who raised a large number of hybrids from a bantam-hen by *Gallus sonneratii*, states that "all were exceedingly wild." Mr. Waterton<sup>44</sup> 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, though 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: but Mr. Jenner Weir who has had still greater experience, is of a directly opposite opinion. He remarks that the siskin is the tamest of finches, but its mules are as wild, when young, as newly caught birds, and are often lost through their continued efforts to escape. 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<sup>45</sup> observed that his hybrids were wild, and exhibited "migratory propensities" of which there is not a vestige in the common or musk duck. No case is known of this latter 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<sup>46</sup> of hybrids from these two ducks having been shot in a completely wild state, although so few are reared in comparison with purely-bred birds of either species. It is improbable that any of these hybrids could have acquired their wildness

<sup>44</sup> 'Essays on Natural History,' p. 917.

<sup>45</sup> As stated by Mr. Orton, in his 'Physiology of Breeding,' p. 12.

<sup>46</sup> M. E. de Selys-Longchamps refers ('Bulletin Acad. Roy. de Bruxelles,' tom. xii. No. 10) to more than seven of these hybrids shot in Switzerland and France. M. Deby asserts ('Zoologist,' vol. v., 1845-46, p. 1254) that several have been shot in various parts of Belgium and Northern France. Audubon ('Ornitholog. Biography,' vol. iii. p. 168), speaking of these hybrids, says that, in North America, they "now and then wander off and become quite wild."

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.<sup>47</sup> 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 halfcastes."<sup>48</sup> When two races, both low in the scale, are crossed the progeny seems to be eminently bad. Thus the noblehearted Humboldt, who felt no prejudice against the inferior races, 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.<sup>49</sup> 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, even if mainly due to the unfavourable moral conditions under which they are generally reared.

Summary on the proximate causes leading to Reversion.—When

<sup>47</sup> 'Journal of Researches,' 1845,
p. 71.
<sup>48</sup> 'Expedition to the Zambesi,'
1865, pp. 25, 150.

<sup>49</sup> Dr. P. Broca, on 'Hybridity in the Genus Homo,' Eng. translat., 1864, p. 39.

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 slatyblue 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 any change in the habits of life apparently favour 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 character proper to the variety, or its reversion to a former state.

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 E. 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<sup>50</sup> 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 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 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 selfaffinity. 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 com-

<sup>50</sup> 'Nouvelles Archives du Muséum,' tom. i. p. 151.

pletely 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 chapter on the hypothesis of 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 highly sterile hybrid plants exhibit any tendency to reversion to their parent-forms. This erroneous belief may perhaps be accounted for by the nature of the genera crossed 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.<sup>51</sup>

Gärtner further states that reversions rarely occur with hybrid plants raised from species 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,<sup>52</sup> 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

<sup>51</sup> 'Bastarderzeugung,'s. 582, 438, &c. <sup>52</sup> 'Die Bastardbefruchtung . . . der Weiden,'1865, s. 23. For Gärtner's remarks on this head, see 'Bastarderzeugung,'s. 474, 582.

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 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.<sup>53</sup>

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 grandparent, 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 or dormant in both parents 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

<sup>53</sup> Prof. Weismann, in his very curious essay on the different forms produced by the same species of butterfly at different seasons ('Saison-Dimorphismus der Schmetterlinge,'pp. 27, 28), has come to a similar conclusion, namely, that any cause which disturbs the organisation, such as the exposure of the cocoons to heat or even to much shaking, gives a tendency to reversion.

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, assume many or all of 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 years than during others.54 A duck ten years old has been known to assume both the perfect winter and summer plumage of the drake.<sup>55</sup> Waterton <sup>56</sup> 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, 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, which often affects the reproductive system, causing analogous results. But cha-

<sup>54</sup> Yarrell, 'Phil. Transact.,' 1827, p. 268; Dr. Hamilton, in 'Proc. Zoolog. Soc.,' 1862, p. 23.

<sup>55</sup> Archiv. Skand. Beiträge zur Naturgesch.' viii. s. 397-413.

<sup>56</sup> In his 'Essays on Nat. Hist.,' 1838, Mr. Hewitt gives analogous cases with hen-pheasants in 'Journal of Horticulture, July 12, 1864, p. 37. Isidore Geoffroy Saint-Hilaire, in his 'Essais de Zoolog. Gén.' ('suites à Buffon,' 1842, pp. 496-513), has collected such cases in ten different kinds of birds. It appears that Aristotle was well aware of the change in mental disposition in old hens. The case of the female deer acquiring horns is given at p. 513.

racters properly confined to the female are likewise acquired by the male; 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." <sup>57</sup> That admirable observer Reaumur <sup>58</sup> 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 shows 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 <sup>59</sup> 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

59 Sir H. Holland, 'Medical Notes and Reflections,' 3rd edit., 1855, p.

<sup>57 &#</sup>x27;Cottage Gardener,' 1860, p. 379. 55 'Art de faire Eclore,' &c., 1749, 31. tom. ii. p. 8.

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 is gradually twisted from the lower to the upper surface.<sup>60</sup> In most flat-fishes the left is the blind side, but in some it is the right; though in both cases reversed or" wrong fishes," are occasionally developed; and in Platessa flesus the right or left side is indifferently the upper one. With gasteropods or shell-fish, the right and left sides are extremely unlike; 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,<sup>61</sup> are as often sinistral as dextral. I will give an analogous case in the great articulate kingdom: the two sides of Verruca<sup>62</sup> 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 amount of change. One plant is known to me 63 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 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 cases of characters lying dormant are, perhaps, those previously given, in which chickens and young pigeons, raised from a cross between differently coloured

<sup>60</sup> See Steenstrup on the 'Obliquity of Flounders': in 'Annals and Mag. of Nat. Hist.' May, 1865, p. 361. I have given an abstract of Malm's explanation of this wonderful phenomenon in the 'Origin of Species' 6th Edit. p. 186.

Edit. p. 186. <sup>61</sup> Dr. E. von Martens, in 'Annals and Mag. of Nat. Hist.' March, 1866, p. 209.

<sup>62</sup> Darwin, 'Balanidæ,' Ray Soc., 1854, p. 499: *see* also the appended remarks on the apparently capricious development of the thoracic limbs on the right and left sides in the higher crustaceans.

<sup>63</sup> Mormodes ignea: Darwin, 'Fertilisation of Orchids,' 1862, p. 251.

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 small horns as they grow old. 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<sup>64</sup> possessed an excellent Sebright gold-laced bantam hen, 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, saddlefeathers 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 <sup>65</sup> 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 henbird, 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 sign of their presence. When fowls, pigeons, or cattle of different colours are crossed, and

Tegetmeier.

<sup>65</sup> 'The Poultry Book,' by Mr. Tegetmeier, 1866, p. 241.

<sup>&</sup>lt;sup>64</sup> 'Journal of Horticulture,' July, 1864, p. 38. I have had the opportunity of examining these remarkable feathers through the kindness of Mr.

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, who 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 in all reversions 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 cccasionally produce by reversion tabbies; and on young black kittens, with a pedigree <sup>66</sup> known to have been long pure, faint traces of stripes may almost always be seen which afterwards dis-Hornless Suffolk cattle occasionally produce by appear. reversion horned animals; and Youatt<sup>67</sup> asserts that even in hornless individuals "the rudiment of a horn may be often felt at an early age."

No doubt it appears at first sight in the highest degree improbable that in every horse of every generation there should

<sup>66</sup> Carl Vogt, 'Lectures.on Man,' <sup>67</sup> 'On Cattle,' p. 174. Eng. translat., 1864, p. 411.

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 to the immediately preceding generations may be constantly observed, at least, 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.

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. But many monstrosities cannot be thus explained; for parts of which no trace can be detected in the embryo, but which occur in other members of the same class of animals occasionally appear, and these may probably with truth be attributed to reversion. As, however, I have treated this subject as fully as I could in my 'Descent of Man' (chap. i., 2nd edit.), I will not here recur to it.

When flowers which have normally an irregular structure become regular or peloric, the change is generally looked at by botanists as a return to the primitive state. But Dr. Maxwell Masters, <sup>68</sup> 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 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 that the parent-form, for instance, of the genus Linaria had had all its petals spurred; for a chance 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,<sup>69</sup> they probably stand in some close relation to one another. On the doctrine that peloria is simply the result of an arrest of development, it is difficult to understand how an organ arrested as 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

<sup>68</sup> 'Natural Hist. Review,' April, 1863, p. 258. See also his Lecture, Royal Institution, March 16, 1860. On same subject, see Moquin-Tandon, 'Éléments de Tératologie,' 1841, pp. 184, 352. Dr. Peyritsch has collected a large number of very interesting

<sup>69</sup> Verlot, 'Des Variétés,' 1865, p. 89; Naudin, 'Nouvelles Archives du Muséum,' tom. i. p. 137.

cases, Sitzb. d. k. Akad. d. Wissensch.: Wien. Bd. LX. and especially Bd, LXVI., 1872, p. 125.

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,<sup>70</sup> 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, as the following interesting case shows. 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 stamen 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.

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 genus Geranium; 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 may look at the peloric flowers of Pelargonium as having 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 of the common snapdragons in the nineteen plants examined

<sup>70</sup> In his discussion on some curious peloric Calceolarias, quoted in 'Jour-

nal of Horticulture,' Feb. 24, 1863, p. 152.

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 the 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.<sup>71</sup> 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. The conclusion that peloria is not a mere monstrosity, irrespective of any former state of the species, is supported by the fact that this structure is often strongly inherited, as in the case of the peloric Antirrhinum and Gloxinia and sometimes in that of the peloric Corydalis solida.<sup>72</sup>

Lastly I may add that many instances have been recorded of flowers, not generally considered as peloric, in which certain organs are abnormally augmented in number. As 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

<sup>72</sup> Godron, reprinted from the 'Mémoires de l'Acad. de Stanislas,' 1868.

<sup>&</sup>lt;sup>11</sup> For other cases of six divisions in peloric flowers of the Labiatæ and Scrophulariaceæ, *see* Moquin-Tandon, 'Tératologie,' p. 192.

parts now in a more or less rudimentary condition, -- the reappearance of organs of which not a vestige can 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 this condition.<sup>73</sup> On this view of the nature of peloric flowers, and bearing in mind certain monstrosities in the animal kingdom, we must conclude that the progenitors of most plants and animals have left an impression, capable of redevelopment, on the germs of their descendants, although these have since been profoundly modified.

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 which it undergoes, we must

<sup>78</sup> Moquin-Tandon, ' Tératologie,' p. 186.

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, lie ready to be evolved whenever the organisation is disturbed by certain known or unknown conditions.