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 last two 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 fully 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 be likely to continue so, if the conditions of life remain the same. 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 able to assign any cause, that, when a new character appears, it is occasionally from the first constant, 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 transmitted and the length of time during which it has 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 organs or parts which in our domesticated productions have varied, or which still continue to vary,—that is, which fail to retain their former 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 one another

have varied, whilst other parts of the organisation have remained unchanged; and it might be argued that these same characters now vary under domestication, or fail to be inherited, from their lesser antiquity. But variation in a state of nature seems to stand in some close relation with changed conditions of life, and characters which have already varied under such conditions would be apt to vary under the still greater changes consequent on domestication, independently of their greater or less antiquity.

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.[1] It has often been observed 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 cumulative 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 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.

[1] *See* Youatt on Cattle, pp. 92, 69, 78, 88, 163; and Youatt on Sheep, p. 325. Also Dr. Lucas, 'L'Héréd. Nat.,' tom. ii. p. 310.

Prepotency in the Transmission of Character.

When individuals, belonging to the same family, but distinct enough to be recognised, 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,[2] but is rendered extremely complex 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 crossed breeds with their parents difficult.

It would appear that in certain families some one ancestor, and after him others in the same family, 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 many females, as in the case of the Austrian Emperors; and so it was, according to Niebuhr, with the mental qualities of certain Roman families.[3] The famous bull Favourite is believed [4] to have had a prepotent influence on the short-horn race. It has also been observed [5] 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. A famous black greyhound, Bedlamite, as I hear from Mr. C. M. Brown "invariably got all his "puppies black, no matter what was the colour of the bitch;" but then Bedlamite "had a preponderance of black in his "blood, both on the sire and dam side."

[2] 'Héréd. Nat.,' tom. ii. pp. 112-120.

[3] Sir H. Holland, 'Chapters on Mental Physiology,' 1852, p. 234.

[4] 'Gardener's Chronicle,' 1860, p. 270.

[5] Mr. N. H. Smith, 'Observations on Breeding,' quoted in 'Encyclop. of Rural Sports,' p. 278.

The truth of the principle of prepotency comes out more clearly when distinct races are crossed. The improved Short-horns, 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.[6] Godine has given a curious case of a ram of a goat-like breed of sheep from the Cape of Good Hope, which produced offspring hardly to be distinguished from himself, when crossed with ewes of twelve other breeds. But two of these half-bred ewes, when put to a merino ram, produced lambs closely resembling the merino breed. Girou de Buzareingues[7] 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.[8]

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 preponderate over fantails. This weakness of transmission in the fantail, though the breed is an ancient one, is said[9] 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 singular 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

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[6] Quoted by Bronn, 'Geschichte der Natur,' b. ii. s. 170. *See* Sturm, 'Ueber Racen,' 1825, s. 104–107. For the niata cattle, *see* my 'Journal of Researches,' 1845, p. 146.

[7] Lucas, 'L'Hérédité Nat.,' tom. ii. p. 112.

[8] Mr. Orton, 'Physiology of Breeding,' 1855, p. 9.

[9] Boitard and Corbié, 'Les Pigeons,' 1824, p. 224.

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[10] assert that this is the invariable result of crossing trumpeters with other breeds: Neumeister,[11] 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[12] that the crossed offspring of a trumpeter were crossed with trumpeters for three generations, by which time the mongrels had 7-8ths of this 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 its 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.[13] 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![14]

The well-known horticulturist, Mr. Paul, informs me that he fertilised the Black Prince hollyhock with pollen of the White Globe and the Lemonade and Black Prince hollyhocks reciprocally; but not one seedling from these three crosses inherited the black colour of the Black Prince. So, again, Mr. Laxton, who has had such great experience in crossing peas, writes to me that "when-ever a cross has been effected between a white-blossomed and a purple-blossomed pea, or between a white-seeded and a purple-spotted, brown or maple-seeded pea, the offspring seems to lose

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[10] 'Les Pigeons,' pp. 168, 198.
[11] 'Das Ganze,' &c., 1837, s. 39.
[12] 'The Pigeon Book,' p. 46.
[13] 'Physiology of Breeding,' p. 22; Mr. Hewitt, in 'The Poultry Book,' by Tegetmeier, 1866, p. 224.
[14] Boitard and Corbié, 'Les Pigeons,' 1824, p. 226.

"nearly all the characteristics of the white-flowered and white-"seeded varieties; and this result follows whether these varieties "have been used as the pollen-bearing or seed-producing parents."

The law of prepotency comes into action when species are crossed, as with races and individuals. Gärtner has unequivocally shown[15] 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 latter 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 a 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.[16] The male pheasant, judging from Mr. Hewitt's descriptions,[17] 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,

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[15] 'Bastarderzeugung,' s. 256, 290, &c. Naudin ('Nouvelles Archives du Muséum,' tom. i. p. 149) gives a striking instance of prepotency in *Datura stramonium* when crossed with two other species.

[16] Flourens, 'Longévité Humaine,' p. 144, on crossed jackals. With respect to the difference between the mule and the hinny, I am aware that this has generally been attributed to the sire and dam transmitting their characters differently; but Colin, who has given in his 'Traité Phys. Comp.,' tom. ii. pp. 537–539, the fullest description which I have met with of these reciprocal hybrids, is strongly of opinion that the ass preponderates in both crosses, but in an unequal degree. This is likewise the conclusion of Flourens, and of Bechstein in his 'Naturgeschichte Deutschlands,' b. i. s. 294. The tail of the hinny is much more like that of the horse than is the tail of the mule, and this is generally accounted for by the males of both species transmitting with greater power this part of their structure; but a compound hybrid which I saw in the Zoological Gardens, from a mare by a hybrid ass-zebra, closely resembled its mother in its tail.

[17] Mr. Hewitt, who has had such great experience in raising these hybrids, says ('Poultry Book,' by Mr. Tegetmeier, 1866, pp. 165–167) that in all, the head was destitute of wattles, comb, and ear-lappets; and all closely resembled the pheasant in the shape of the tail and general contour of the body. These hybrids were raised from hens of several breeds by a cock-pheasant; but another hybrid, described by Mr. Hewitt, was raised from a hen-pheasant, by a silver-laced Bantam cock, and this possessed a rudimental comb and wattles.

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 (*Anser ægyptiacus*); 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 its 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[18] that none of the rules (and I could add others to those quoted by him) apply to all animals. Similar rules have been announced for plants, and have been proved by Gärtner[19] 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;[20] but conspicuous exceptions have passed under my own eyes. 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.

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,

[18] 'L'Héréd. Nat.,' tom. ii. book ii. ch. i.

[19] 'Bastarderzeugung,' s. 264–266. Naudin ('Nouvelles Archives du Muséum,' tom. i. p. 148) has arrived at a similar conclusion.

[20] 'Cottage Gardener,' 1856, pp. 101, 137.

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 mongrelised and already variable form.[21] 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 breeds 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 white 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, develope 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.

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

[21] *See* some remarks on this head with respect to sheep by Mr. Wilson, in 'Gardener's Chronicle,' 1863, p. 15. Many striking instances of this result are given by M. Malingié-Nouel ('Journ. R. Agricult. Soc.,' vol. xiv. 1853, p. 220) with respect to crosses between English and French sheep. He found that he obtained the desired influence of the English breeds by crossing intentionally mongrelised French breeds with pure English breeds.

produce striped seedlings.[22] Another case is in some respects more curious: plants bearing peloric 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.[23] 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 [24] 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 peloric, having reverted to the structure of their one grandparent. This case seems at first sight to offer an exception to the rule just 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

[22] Verlot, 'Des Variétés,' 1865, p. 66.
[23] Moquin-Tandon, 'Tératologie,' p. 191.
[24] 'Nouvelles Archives du Muséum,' tom. i. p. 137.

in the last chapter, a strong latent tendency to become peloric; but there is also, as we have 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 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 no one has hitherto succeeded 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 directly connected with the organs of reproduction, are conspicuously present. With our domesticated animals, characters of this kind often differ widely from those distinguishing the two sexes of the parent species; and the principle of inheritance, as limited by sex, explains how this is possible.

Dr. P. Lucas has shown[25] 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 the 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 the very same peculiarity may become attaced 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 tends to be transmitted in a greater or lesser degree to that sex in which it first appears. But a more definite rule, as I have elsewhere shown,[26] generally holds good, namely, that variations which first appear in either sex at a late period of life, when the reproductive functions are active, tend to be developed in that sex alone; whilst variations which first appear early in life in either sex are commonly transmitted to both sexes. I am, however, far from supposing that this is the sole determining cause.

A few details from the many cases collected by Mr. Sedgwick,[27] 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-blindness thus generally clings to the male sex,

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[25] 'L'Héréd. Nat.,' tom. ii. pp. 137-165. *See*, also, Mr. Sedgwick's four memoirs, immediately to be referred to.

[26] 'Descent of Man,' 2nd edit., p. 32.

[27] On Sexual Limitation in Hereditary Diseases, 'Brit. and For. Med.-Chirurg. Review,' April 1861, p. 477; July, p. 198; April 1863, p. 445; and July, p. 159. Also in 1867, 'On the influence of Age in Hereditary Disease.'

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. The 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 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-grand-daughter 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; they differ also in the development of fat in the tail 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,[28] and, judging from analogy, more than in the aboriginal parent-species. The peculiar colour called tortoise-

[28] W. Scrope, 'Art of Deer Stalking,' p. 354.

shell is very rarely seen in a male cat; the males of this variety being of a rusty tint.

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 of 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 shaded with black, 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 throughout the whole great family the two sexes do not often differ much; 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 the males alone are spotted or striated with black, or otherwise differ in colour. 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 belong to the species in a state of nature 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 Hamburg 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,[29] and afterwards to be inherited exclusively or more strongly by the males. Finally, in accordance with the principle of inheritance as limited by sex, the preservation and augmentation of secondary sexual characters in natural species offers no especial difficulty, as this would follow through that form of selection which I have called sexual selection.

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 one of the most remarkable 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 after the parent-form has undergone great 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 one another and probably like their common progenitor. We can thus understand why embryology throws a flood of light on the natural system of classification, as 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 one another and with

[29] I have given in my 'Descent of Man' (2nd edit. p. 223) sufficient evidence that male animals are usually more variable than the females.

their parent-forms, present conspicuous differences, both in their 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 whilst covered with down, in the plumage at the first and subsequent moults, as well as in the comb and wattles, are all inherited. With man peculiarities in the milk and second teeth (of which I have received the details) are inheritable, and 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.

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.[30] In the extraordinary hairy family described by Mr. Crawfurd,[31] 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.

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 brace of pigeons in which the whole body is white except the breast, neck, and head; but in their first plumage all the white feathers have 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 become 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.[32] 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."[33] A curious and somewhat analogous account has been given[34] 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 are inherited at various corresponding periods of life in the pigeon, canary-bird, and rook, are remarkable, because the parent-species passes through no such change.

Inherited diseases afford evidence in some respects of less value

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[30] Prichard, 'Phys. Hist. of Mankind,' 1851, vol. i. p. 349.

[31] 'Embassy to the Court of Ava,' vol. i. p. 320. The third generation is described by Capt. Yule in his 'Narrative of the Mission to the Court of Ava,' 1855, p. 94.

[32] 'Das Ganze der Taubenzucht,' 1837, s. 24, tab. iv., fig. 2; s. 21, tab. i., fig. 4.

[33] Kidd's 'Treatise on the Canary,' p. 18.

[34] Charlesworth, 'Mag. of Nat. Hist.,' vol. i. 1837, p. 167.

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 tendency to the disease is inheritable.[35] 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[36] cautions the physician to look closely to the child at the period when any grave inheritable disease attacked the parent. Dr. Prosper Lucas,[37] 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 through three generations, and no less than twenty-seven children and grandchildren were all affected at about the same age; their blindness in general began to advance about the fifteenth or sixteenth year, and ended in total deprivation of sight at the age of about twenty-two.[38] 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.[39]

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[35] Dr. Prosper Lucas, 'Héréd. Nat.,' tom. ii. p. 713.

[36] 'L'Héréd. dans les Maladies,' 1840, p. 135. For Hunter, *see* Harlan's 'Med. Researches,' p. 530.

[37] 'L'Héréd. Nat.,' tom. ii. p. 850.

[38] Sedgwick, 'Brit. and For. Med.-Chirurg. Review,' April, 1861, p. 485. In some accounts the number of children and grandchildren is given as 37; but this seems to be an error judging from the paper first published in the 'Baltimore Med. and Phys. Reg.' 1809, of which Mr. Sedgwick has been so kind as to send me a copy.

[39] Prosper Lucas, 'Héréd. Nat.' tom. i. p. 400.

So with deafness, two brothers, their father and paternal grandfather, all became deaf at the age of forty.[40]

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.[41] 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.[42] 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, such 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.[43]

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 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.[44]

It is impossible to read the foregoing accounts, and the many others which have been recorded, of diseases coming

[40] Sedgwick, ibid., July, 1861, p. 202.

[41] Piorry, p. 109; Prosper Lucas, tom. ii. p. 759.

[42] Prosper Lucas, tom. ii. p. 748.

[43] Prosper Lucas, tom. iii. pp. 678, 700, 702; Sedgwick, ibid., April, 1863, p. 449, and July, 1863, p. 162, Dr. J. Steinan, 'Essay on Hereditary Disease,' 1843, pp. 27, 34.

[44] These cases are given by Mr. Sedgwick, on the authority of Dr. H. Stewart, in 'Med.-Chirurg. Review,' April, 1863, pp. 449, 477.

on during three or even more generations in several members of the same family at the same age, especially in the case of rare affections in which the coincidence cannot be attributed to chance, and to 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 very much rarer. Dr. Lucas[45] 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: Sir J. Paget, who has particularly attended to this subject, and tabulated a large number of cases, informs me that he believes 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 influencing the fatal period in the offspring; 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 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 its proper character at too early an age.

[45] 'Héréd. Nat.,' tom. ii. p. 852.

Finally, from the numerous races of cultivated plants and domestic animals, in which the seeds or eggs, the young or old, differ from one another and from those of the parent-species;—from the cases in which new characters have appeared at a particular period, and afterwards 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 monstrosity,—or so peculiar as not to occur normally in any member of the same natural class,—are often inherited by man, by 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 ample evidence that the effects of mutilations and of accidents, especially or perhaps exclusively when followed by disease, are occasionally inherited. There can be no doubt that the evil effects of the long-continued exposure of 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 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 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 certain conditions.

What these conditions precisely are, we do not know. But any cause which disturbs the organisation or constitution seems to be sufficient. A cross certainly gives a strong tendency to the reappearance of long-lost characters, both corporeal and mental. In the case of plants, this tendency is much stronger with those species which have been crossed after long cultivation and which therefore have had their constitutions disturbed by this cause as well as by crossing, than with species which have always lived under their natural conditions and have then been crossed. A return, also, of domesticated animals and cultivated plants to a wild state favours reversion; but the tendency under these circumstances has been much exaggerated.

When individuals of the same family which differ somewhat, and when races or species are crossed, the one is often

prepotent over the other in transmitting its 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. Prepotency 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, 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 see how secondary sexual characters may 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 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. Fourthly, transmission, as limited by sex, generally to the same sex in which the inherited character first appeared; and this in many, probably most cases, depends on the new character having first appeared at a rather late period of life. 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.