

# Laws of Variation

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# Effects of Changed Conditions

I have hitherto sometimes spoken as if the variations — so common and multiform with organic beings under domestication, and in a lesser degree with those under nature — were due to chance. This, of course is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation. Some authors believe it to be as much the function of the reproductive system to produce individual differences, or slight deviations of structure, as to make the child like its parents. But the fact of variations and monstrosities occurring much more frequently under domestication than under nature, and the greater variability of species having wide ranges than of those with restricted ranges, lead to the conclusion that variability is generally related to the conditions of life to which each species has been exposed during several successive generations. In the first chapter I attempted to show that changed conditions act in two ways, directly on the whole organisation or on certain parts alone, and indirectly through the reproductive system. In all cases there are two factors, the nature of the organism, which is much the most important of the two, and the nature of the conditions. The direct action of changed conditions leads to definite or indefinite results. In the latter case the organisation seems to become plastic, and we have much fluctuating variability. In the former case the nature of the organism is such that it yields readily, when subjected to certain conditions, and all, or nearly all, the individuals become modified in the same way.

It is very difficult to decide how far changed conditions, such as of climate, food, &c., have acted in a definite manner. There is reason to believe that in the course of time the effects have been greater than can be proved by clear evidence. But we may safely conclude that the innumerable complex co-adaptations of structure, which we see throughout nature between various organic beings, cannot be attributed simply to such action. In the following cases the conditions seem to have produced some slight definite effect: E. Forbes asserts that shells at their southern limit, and when living in shallow water, are more brightly coloured than those of the same species from further north or from a greater depth; but this certainly does not always hold good. Mr. Gould believes that birds of the same species are more brightly coloured under a clear atmosphere, than when living near the coast or on islands; and Wollaston is convinced that residence near the sea affects the colours of insects. Moquin-Tandon gives a list of plants which, when growing near the sea-shore, have their leaves in some degree fleshy, though not elsewhere fleshy. These slightly varying organisms are interesting in as far as they present characters analogous to those possessed by the species which are confined to similar conditions.

When a variation is of the slightest use to any being, we cannot tell how much to attribute to the accumulative action of natural selection, and how much to the definite action of the conditions of life. Thus, it is well known to furriers that animals of the same species have thicker and better fur the further north they live; but who can tell how much of this difference may be due to the warmest-clad individuals having been favoured and preserved during many generations, and how much to the action of the severe climate? For it would appear that climate has some direct action on the hair of our domestic quadrupeds.

Instances could be given of similar varieties being produced from the same species under external conditions of life as different as can well be conceived; and, on the other hand, of dissimilar varieties being produced under apparently the same external conditions. Again, innumerable instances are known to every naturalist, of species keeping true, or not varying at all, although living under the most opposite climates. Such considerations as these incline me to lay less weight on the direct action of the

surrounding conditions, than on a tendency to vary, due to causes of which we are quite ignorant.

In one sense the conditions of life may be said, not only to cause variability, either directly or indirectly, but likewise to include natural selection, for the conditions determine whether this or that variety shall survive. But when man is the selecting agent, we clearly see that the two elements of change are distinct; variability is in some manner excited, but it is the will of man which accumulates the variations in certain direction; and it is this latter agency which answers to the survival of the fittest under nature.

# Effects of the increased use and disuse of parts, as controlled by natural selection.

From the facts alluded to in the first chapter, I think there can be no doubt that use in our domestic animals has strengthened and enlarged certain parts, and disuse diminished them; and that such modifications are inherited. Under free nature we have no standard of comparison by which to judge of the effects of long-continued use or disuse, for we know not the parent-forms; but many animals possess structures which can be best explained by the effects of disuse. As Professor Owen has remarked, there is no greater anomaly in nature than a bird that cannot fly; yet there are several in this state. The logger-headed duck of South America can only flap along the surface of the water, and has its wings in nearly the same condition as the domestic Aylesbury duck: it is a remarkable fact that the young birds, according to Mr. Cunningham, can fly, while the adults have lost this power. As the larger ground-feeding birds seldom take flight except to escape danger, it is probable that the nearly wingless condition of several birds, now inhabiting or which lately inhabited several oceanic islands, tenanted by no beasts of prey, has been caused by disuse. The ostrich indeed inhabits continents, and is exposed to danger from which it cannot escape by flight, but it can defend itself, by kicking its enemies, as efficiently as many quadrupeds. We may believe that the progenitor of the ostrich genus had habits like those of the bustard, and that, as the size and weight of its body were increased during successive generations, its legs were used more and its wings less, until they became incapable of flight.

Kirby has remarked (and I have observed the same fact) that the anterior tarsi, or feet, of many male dung-feeding beetles are often broken off; he examined seventeen specimens in his own collection, and not one had even a relic left. In the *Onites* apelles the tarsi are so habitually lost that the insect has been described as not having them. In some other genera they are present, but in a rudimentary condition. In the *Ateuchus* or sacred beetle of the Egyptians, they are totally deficient. The evidence that accidental mutilations can be inherited is at present not decisive; but the remarkable cases observed by Brown-Séguard in guinea-pigs, of the inherited effects of operations, should make us cautious in denying this tendency. Hence, it will perhaps be safest to look at the entire absence of the anterior tarsi in *Ateuchus*, and their rudimentary condition in some other genera, not as cases of inherited mutilations, but as due to the effects of long-continued disuse; for as many dung-feeding beetles are generally found with their tarsi lost, this must happen early in life; therefore the tarsi cannot be of much importance or be much used by these insects.

In some cases we might easily put down to disuse modifications of structure which are wholly, or mainly due to natural selection. Mr. Wollaston has discovered the remarkable fact that 200 beetles, out of the 550 species (but more are now known) inhabiting Madeira, are so far deficient in wings that they cannot fly; and that, of the twenty-nine endemic genera, no less than twenty-three have all their species in this condition! Several facts,— namely, that beetles in many parts of the world are very frequently blown to sea and perish; that the beetles in Madeira, as observed by Mr. Wollaston, lie much concealed, until the wind lulls and the sun shines; that the proportion of wingless beetles is larger on the exposed Desertas than in Madeira itself; and especially the extraordinary fact, so strongly insisted on by Mr. Wollaston, that certain large groups of beetles, elsewhere excessively numerous, which absolutely require the use of their wings, are here almost entirely absent;— these several considerations make me believe that the wingless condition of so many Madeira beetles is mainly due

to the action of natural selection, combined probably with disuse. For during many successive generations each individual beetle which flew least, either from its wings having been ever so little less perfectly developed or from indolent habit, will have had the best chance of surviving from not being blown out to sea; and, on the other hand, those beetles which most readily took to flight would oftenest have been blown to sea, and thus destroyed.

The insects in Madeira which are not ground-feeders, and which, as certain flower-feeding coleoptera and lepidoptera, must habitually use their wings to gain their subsistence, have, as Mr. Wollaston suspects, their wings not at all reduced, but even enlarged. This is quite compatible with the action of natural selection. For when a new insect first arrived on the island, the tendency of natural selection to enlarge or to reduce the wings, would depend on whether a greater number of individuals were saved by successfully battling with the winds, or by giving up the attempt and rarely or never flying. As with mariners shipwrecked near a coast, it would have been better for the good swimmers if they had been able to swim still further, whereas it would have been better for the bad swimmers if they had not been able to swim at all and had stuck to the wreck.

The eyes of moles and of some burrowing rodents are rudimentary in size, and in some cases are quite covered by skin and fur. This state of the eyes is probably due to gradual reduction from disuse, but aided perhaps by natural selection. In South America, a burrowing rodent, the tuco-tuco, or *Ctenomys*, is even more subterranean in its habits than the mole; and I was assured by a Spaniard, who had often caught them, that they were frequently blind. One which I kept alive was certainly in this condition, the cause, as appeared on dissection, having been inflammation of the nictitating membrane. As frequent inflammation of the eyes must be injurious to any animal, and as eyes are certainly not necessary to animals having subterranean habits, a reduction in their size, with the adhesion of the eyelids and growth of fur over them, might in such case be an advantage; and if so, natural selection would aid the effects of disuse.

It is well known that several animals, belonging to the most different classes, which inhabit the caves of Carniola and Kentucky, are blind. In some of the crabs the foot-stalk for the eye remains, though the eye is gone;— the stand for the telescope is there, though the telescope with its glasses has been lost. As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, their loss may be attributed to disuse. In one of the blind animals, namely, the cave-rat (*Neotoma*), two of which were captured by Professor Silliman at above half a mile distance from the mouth of the cave, and therefore not in the profoundest depths, the eyes were lustrous and of large size; and these animals, as I am informed by Professor Silliman, after having been exposed for about a month to a graduated light, acquired a dim perception of objects.

It is difficult to imagine conditions of life more similar than deep limestone caverns under a nearly similar climate; so that, in accordance with the old view of the blind animals having been separately created for the American and European caverns, very close similarity in their organisation and affinities might have been expected. This is certainly not the case if we look at the two whole faunas; with respect to the insects alone, Schiödte has remarked: "We are accordingly prevented from considering the entire phenomenon in any other light than something purely local, and the similarity which is exhibited in a few forms between the Mammoth Cave (in Kentucky) and the caves in Carniola, otherwise than as a very plain expression of that analogy which subsists generally between the fauna of Europe and of North America." On my view we must suppose that American animals, having in most cases ordinary powers of vision, slowly migrated by successive generations from the outer world into the deeper and deeper recesses of the Kentucky caves, as did European animals into

the caves of Europe. We have some evidence of this gradation of habit; for, as Schiödte remarks: "We accordingly look upon the subterranean faunas as small ramifications which have penetrated into the earth from the geographically limited faunas of the adjacent tracts, and which, as they extended themselves into darkness, have been accommodated to surrounding circumstances. Animals not far remote from ordinary forms, prepare the transition from light to darkness. Next follow those that are constructed for twilight; and, last of all, those destined for total darkness, and whose formation is quite peculiar." These remarks of Schiödte's, it should be understood, apply not to the same, but to distinct species. By the time that an animal had reached, after numberless generations, the deepest recesses, disuse will on this view have more or less perfectly obliterated its eyes, and natural selection will often have effected other changes, such as an increase in the length of the antennæ or palpi, as a compensation for blindness. Notwithstanding such modifications, we might expect still to see in the cave-animals of America, affinities to the other inhabitants of that continent, and in those of Europe to the inhabitants of the European continent. And this is the case with some of the American cave-animals, as I hear from Professor Dana; and some of the European cave-insects are very closely allied to those of the surrounding country. It would be difficult to give any rational explanation of the affinities of the blind cave-animals to the other inhabitants of the two continents on the ordinary view of their independent creation. That several of the inhabitants of the caves of the Old and New Worlds should be closely related, we might expect from the well-known relationship of most of their other productions. As a blind species of *Bathyscia* is found in abundance on shady rocks far from caves, the loss of vision in the cave species of this one genus has probably had no relation to its dark habitation; for it is natural that an insect already deprived of vision should readily become adapted to dark caverns. Another blind genus (*Anophthalmus*) offers this remarkable peculiarity, that the species, as Mr. Murray observes, have not as yet been found anywhere except in caves; yet those which inhabit the several caves of Europe and America are distinct; but it is possible that the progenitors of these several species, while they were furnished with eyes, may formerly have ranged over both continents, and then have become extinct, excepting in their present secluded abodes. Far from feeling surprise that some of the cave-animals should be very anomalous, as Agassiz has remarked in regard to the blind fish, the *Amblyopsis*, and as is the case with the blind *Proteus*, with reference to the reptiles of Europe, I am only surprised that more wrecks of ancient life have not been preserved, owing to the less severe competition to which the scanty inhabitants of these dark abodes will have been exposed.

# Acclimatisation.

Habit is hereditary with plants, as in the period of flowering, in the time of sleep, in the amount of rain requisite for seeds to germinate, &c., and this leads me to say a few words on acclimatisation. As it is extremely common for distinct species belonging to the same genus to inhabit hot and cold countries, if it be true that all the species of the same genus are descended from a single parent-form, acclimatisation must be readily effected during a long course of descent. It is notorious that each species is adapted to the climate of its own home: species from an arctic or even from a temperate region cannot endure a tropical climate, or conversely. So again, many succulent plants cannot endure a damp climate. But the degree of adaptation of species to the climates under which they live is often overrated. We may infer this from our frequent inability to predict whether or not an imported plant will endure our climate, and from the number of plants and animals brought from different countries which are here perfectly healthy. We have reason to believe that species in a state of nature are closely limited in their ranges by the competition of other organic beings quite as much as, or more than, by adaptation to particular climates. But whether or not this adaptation is in most cases very close, we have evidence with some few plants, of their becoming, to a certain extent, naturally habituated to different temperatures; that is, they become acclimatised: thus the pines and rhododendrons, raised from seed collected by Dr. Hooker from the same species growing at different heights on the Himalayas, were found to possess in this country different constitutional powers of resisting cold. Mr. Thwaites informs me that he has observed similar facts in Ceylon; analogous observations have been made by Mr. H. C. Watson on European species of plants brought from the Azores to England; and I could give other cases. In regard to animals, several authentic instances could be adduced of species having largely extended, within historical times, their range from warmer to cooler latitudes, and conversely; but we do not positively know that these animals were strictly adapted to their native climate, though in all ordinary cases we assume such to be the case; nor do we know that they have subsequently become specially acclimatised to their new homes, so as to be better fitted for them than they were at first.

As we may infer that our domestic animals were originally chosen by uncivilised man because they were useful, and because they bred readily under confinement, and not because they were subsequently found capable of far-extended transportation, the common and extraordinary capacity in our domestic animals of not only withstanding the most different climates, but of being perfectly fertile (a far severer test) under them, may be used as an argument that a large proportion of other animals now in a state of nature could easily be brought to bear widely different climates. We must not, however, push the foregoing argument too far, on account of the probable origin of some of our domestic animals from several wild stocks: the blood, for instance, of a tropical and arctic wolf may perhaps be mingled in our domestic breeds. The rat and mouse cannot be considered as domestic animals, but they have been transported by man to many parts of the world, and now have a far wider range than any other rodent; for they live under the cold climate of Faroe in the north and of the Falklands in the south, and on many an island in the torrid zones. Hence adaptation to any special climate may be looked at as a quality readily grafted on an innate wide flexibility of constitution, common to most animals. On this view, the capacity of enduring the most different climates by man himself and by his domestic animals, and the fact of the extinct elephant and rhinoceros having formerly endured a glacial climate, whereas the living species are now all tropical or sub-tropical in their habits, ought not to be looked at as anomalies, but as examples of a very common flexibility of constitution, brought, under peculiar circumstances, into action.

How much of the acclimatisation of species to any peculiar climate is due to mere habit, and how much to the natural selection of varieties having different innate constitutions, and how much to both means combined, is an obscure question. That habit or custom has some influence, I must believe, both from analogy and from the incessant advice given in agricultural works, even in the ancient Encyclopædias of China, to be very cautious in transporting animals from one district to another. And as it is not likely that man should have succeeded in selecting so many breeds and sub-breeds with constitutions specially fitted for their own districts, the result must, I think, be due to habit. On the other hand, natural selection would inevitably tend to preserve those individuals which were born with constitutions best adapted to any country which they inhabited. In treatises on many kinds of cultivated plants, certain varieties are said to withstand certain climates better than others; this is strikingly shown in works on fruit-trees published in the United States, in which certain varieties are habitually recommended for the northern and others for the southern states; and as most of these varieties are of recent origin, they cannot owe their constitutional differences to habit. The case of the Jerusalem artichoke, which is never propagated in England by seed, and of which, consequently, new varieties have not been produced, has even been advanced, as proving that acclimatisation cannot be effected, for it is now as tender as ever it was! The case, also, of the kidney-bean has been often cited for a similar purpose, and with much greater weight; but until some one will sow, during a score of generations, his kidney-beans so early that a very large proportion are destroyed by frost, and then collect seed from the few survivors, with care to prevent accidental crosses, and then again get seed from these seedlings, with the same precautions, the experiment cannot be said to have been even tried. Nor let it be supposed that differences in the constitution of seedling kidney-beans never appear, for an account has been published how much more hardy some seedlings are than others; and of this fact I have myself observed striking instances.

On the whole, we may conclude that habit, or use and disuse, have, in some cases, played a considerable part in the modification of the constitution and structure; but that the effects have often been largely combined with, and sometimes overmastered by, the natural selection of innate variations.

# Correlated variation.

I mean by this expression that the whole organisation is so tied together, during its growth and development, that when slight variations in any one part occur and are accumulated through natural selection, other parts become modified. This is a very important subject, most imperfectly understood, and no doubt wholly different classes of facts may be here easily confounded together. We shall presently see that simple inheritance often gives the false appearance of correlation. One of the most obvious real cases is, that variations of structure arising in the young or larvæ naturally tend to affect the structure of the mature animal. The several parts which are homologous, and which, at an early embryonic period, are identical in structure, and which are necessarily exposed to similar conditions, seem eminently liable to vary in a like manner: we see this in the right and left sides of the body varying in the same manner; in the front and hind legs, and even in the jaws and limbs, varying together, for the lower jaw is believed by some anatomists to be homologous with the limbs. These tendencies, I do not doubt, may be mastered more or less completely by natural selection: thus a family of stags once existed with an antler only on one side; and if this had been of any great use to the breed, it might probably have been rendered permanent by natural selection.

Homologous parts, as has been remarked by some authors, tend to cohere; this is often seen in monstrous plants: and nothing is more common than the union of homologous parts in normal structures, as in the union of the petals into a tube. Hard parts seem to affect the form of adjoining soft parts; it is believed by some authors that with birds the diversity in the shape of the pelvis causes the remarkable diversity in the shape of the kidneys. Others believe that the shape of the pelvis in the human mother influences by pressure the shape of the head of the child. In snakes, according to Schlegel, the shape of the body and the manner of swallowing determine the position and form of several of the most important viscera.

The nature of the bond is frequently quite obscure. M. Is. Geoffroy St. Hilaire has forcibly remarked that certain malconformations frequently, and that others rarely, co-exist without our being able to assign any reason. What can be more singular than the relation in cats between complete whiteness and blue eyes with deafness, or between the tortoise-shell colour and the female sex; or in pigeons, between their feathered feet and skin betwixt the outer toes, or between the presence of more or less down on the young pigeon when first hatched, with the future colour of its plumage; or, again, the relation between the hair and the teeth in the naked Turkish dog, though here no doubt homology comes into play? With respect to this latter case of correlation, I think it can hardly be accidental that the two orders of mammals which are most abnormal in their dermal covering, viz., Cetacea (whales) and Edentata (armadilloes, scaly ant-eaters, &c.), are likewise on the whole the most abnormal in their teeth, but there are so many exceptions to this rule, as Mr. Mivart has remarked, that it has little value.

I know of no case better adapted to show the importance of the laws of correlation and variation, independently of utility, and therefore of natural selection, than that of the difference between the outer and inner flowers in some Compositous and Umbelliferous plants. Everyone is familiar with the difference between the ray and central florets of, for instance, the daisy, and this difference is often accompanied with the partial or complete abortion of the reproductive organs. But in some of these plants the seeds also differ in shape and sculpture. These differences have sometimes been attributed to the pressure of the involucre on the florets, or to their mutual pressure, and the shape of the seeds in the ray-florets of some Compositæ countenances this idea; but with the Umbelliferæ it is by no means,

as Dr. Hooker informs me, the species with the densest heads which most frequently differ in their inner and outer flowers. It might have been thought that the development of the ray-petals, by drawing nourishment from the reproductive organs causes their abortion; but this can hardly be the sole case, for in some *Compositæ* the seeds of the outer and inner florets differ, without any difference in the corolla. Possibly these several differences may be connected with the different flow of nutriment towards the central and external flowers. We know, at least, that with irregular flowers those nearest to the axis are most subject to *peloria*, that is to become abnormally symmetrical. I may add, as an instance of this fact, and as a striking case of correlation, that in many *pelargoniums* the two upper petals in the central flower of the truss often lose their patches of darker colour; and when this occurs, the adherent nectary is quite aborted, the central flower thus becoming *peloric* or regular. When the colour is absent from only one of the two upper petals, the nectary is not quite aborted but is much shortened.

With respect to the development of the corolla, Sprengel's idea that the ray-florets serve to attract insects, whose agency is highly advantageous, or necessary for the fertilisation of these plants, is highly probable; and if so, natural selection may have come into play. But with respect to the seeds, it seems impossible that their differences in shape, which are not always correlated with any difference in the corolla, can be in any way beneficial; yet in the *Umbelliferæ* these differences are of such apparent importance — the seeds being sometimes *orthospermous* in the exterior flowers and *coelospermous* in the central flowers,— that the elder De Candolle founded his main divisions in the order on such characters. Hence modifications of structure, viewed by systematists as of high value, may be wholly due to the laws of variation and correlation, without being, as far as we can judge, of the slightest service to the species.

We may often falsely attribute to correlated variation structures which are common to whole groups of species, and which in truth are simply due to inheritance; for an ancient progenitor may have acquired through natural selection some one modification in structure, and, after thousands of generations, some other and independent modification; and these two modifications, having been transmitted to a whole group of descendants with diverse habits, would naturally be thought to be in some necessary manner correlated. Some other correlations are apparently due to the manner in which natural selection can alone act. For instance, Alph. De Candolle has remarked that winged seeds are never found in fruits which do not open; I should explain this rule by the impossibility of seeds gradually becoming winged through natural selection, unless the capsules were open; for in this case alone could the seeds, which were a little better adapted to be wafted by the wind, gain an advantage over others less well fitted for wide dispersal.

# Compensation and Economy of Growth.

The elder Geoffroy and Goethe propounded, at about the same time, their law of compensation or balancement of growth; or, as Goethe expressed it, "in order to spend on one side, nature is forced to economise on the other side." I think this holds true to a certain extent with our domestic productions: if nourishment flows to one part or organ in excess, it rarely flows, at least in excess, to another part; thus it is difficult to get a cow to give much milk and to fatten readily. The same varieties of the cabbage do not yield abundant and nutritious foliage and a copious supply of oil-bearing seeds. When the seeds in our fruits become atrophied, the fruit itself gains largely in size and quality. In our poultry, a large tuft of feathers on the head is generally accompanied by a diminished comb, and a large beard by diminished wattles. With species in a state of nature it can hardly be maintained that the law is of universal application; but many good observers, more especially botanists, believe in its truth. I will not, however, here give any instances, for I see hardly any way of distinguishing between the effects, on the one hand, of a part being largely developed through natural selection and another and adjoining part being reduced by the same process or by disuse, and, on the other hand, the actual withdrawal of nutriment from one part owing to the excess of growth in another and adjoining part.

I suspect, also, that some of the cases of compensation which have been advanced, and likewise some other facts, may be merged under a more general principle, namely, that natural selection is continually trying to economise in every part of the organisation. If under changed conditions of life a structure, before useful, becomes less useful, its diminution will be favoured, for it will profit the individual not to have its nutriment wasted in building up a useless structure. I can thus only understand a fact with which I was much struck when examining cirripedes, and of which many other instances could be given: namely, that when a cirripede is parasitic within another cirripede and is thus protected, it loses more or less completely its own shell or carapace. This is the case with the male *Ibla*, and in a truly extraordinary manner with the *Proteolepas*: for the carapace in all other cirripedes consists of the three highly important anterior segments of the head enormously developed, and furnished with great nerves and muscles; but in the parasitic and protected *Proteolepas*, the whole anterior part of the head is reduced to the merest rudiment attached to the bases of the prehensile antennæ. Now the saving of a large and complex structure, when rendered superfluous, would be a decided advantage to each successive individual of the species; for in the struggle for life to which every animal is exposed, each would have a better chance of supporting itself, by less nutriment being wasted.

Thus, as I believe, natural selection will tend in the long run to reduce any part of the organisation, as soon as it becomes, through changed habits, superfluous, without by any means causing some other part to be largely developed in a corresponding degree. And conversely, that natural selection may perfectly well succeed in largely developing an organ without requiring as a necessary compensation the reduction of some adjoining part.

# Multiple, Rudimentary, and Lowly-organised Structures are Variable.

It seems to be a rule, as remarked by Is. Geoffroy St. Hilaire, both with varieties and species, that when any part or organ is repeated many times in the same individual (as the vertebræ in snakes, and the stamens in polyandrous flowers) the number is variable; whereas the number of the same part or organ, when it occurs in lesser numbers, is constant. The same author as well as some botanists, have further remarked that multiple parts are extremely liable to vary in structure. As "vegetative repetition," to use Professor Owen's expression, is a sign of low organisation; the foregoing statements accord with the common opinion of naturalists, that beings which stand low in the scale of nature are more variable than those which are higher. I presume that lowness here means that the several parts of the organisation have been but little specialised for particular functions; and as long as the same part has to perform diversified work, we can perhaps see why it should remain variable, that is, why natural selection should not have preserved or rejected each little deviation of form so carefully as when the part has to serve for some one special purpose. In the same way that a knife which has to cut all sorts of things may be of almost any shape; whilst a tool for some particular purpose must be of some particular shape. Natural selection, it should never be forgotten, can act solely through and for the advantage of each being.

Rudimentary parts, as is generally admitted, are apt to be highly variable. We shall have to recur to this subject; and I will here only add that their variability seems to result from their uselessness, and consequently from natural selection having had no power to check deviations in their structure.

# **A Part developed in any Species in an extraordinary degree or manner, in comparison with the same Part in allied Species, tends to be highly variable.**

Several years ago I was much struck by a remark to the above effect made by Mr. Waterhouse. Professor Owen, also, seems to have come to a nearly similar conclusion. It is hopeless to attempt to convince any one of the truth of the above proposition without giving the long array of facts which I have collected, and which cannot possibly be here introduced. I can only state my conviction that it is a rule of high generality. I am aware of several causes of error, but I hope that I have made due allowances for them. It should be understood that the rule by no means applies to any part, however unusually developed, unless it be unusually developed in one species or in a few species in comparison with the same part in many closely allied species. Thus, the wing of the bat is a most abnormal structure in the class of mammals; but the rule would not apply here, because the whole group of bats possesses wings; it would apply only if some one species had wings developed in a remarkable manner in comparison with the other species of the same genus. The rule applies very strongly in the case of secondary sexual characters, when displayed in any unusual manner. The term, secondary sexual characters, used by Hunter, relates to characters which are attached to one sex, but are not directly connected with the act of reproduction. The rule applies to males and females; but more rarely to females, as they seldom offer remarkable secondary sexual characters. The rule being so plainly applicable in the case of secondary sexual characters, may be due to the great variability of these characters, whether or not displayed in any unusual manner — of which fact I think there can be little doubt. But that our rule is not confined to secondary sexual characters is clearly shown in the case of hermaphrodite cirripedes; I particularly attended to Mr. Waterhouse's remark, whilst investigating this order, and I am fully convinced that the rule almost always holds good. I shall, in a future work, give a list of all the more remarkable cases. I will here give only one, as it illustrates the rule in its largest application. The opercular valves of sessile cirripedes (rock barnacles) are, in every sense of the word, very important structures, and they differ extremely little even in distinct genera; but in the several species of one genus, *Pyrgoma*, these valves present a marvellous amount of diversification; the homologous valves in the different species being sometimes wholly unlike in shape; and the amount of variation in the individuals of the same species is so great that it is no exaggeration to state that the varieties of the same species differ more from each other in the characters derived from these important organs, than do the species belonging to other distinct genera.

As with birds the individuals of the same species, inhabiting the same country, vary extremely little, I have particularly attended to them; and the rule certainly seems to hold good in this class. I cannot make out that it applies to plants, and this would have seriously shaken my belief in its truth, had not the great variability in plants made it particularly difficult to compare their relative degrees of variability.

When we see any part or organ developed in a remarkable degree or manner in a species, the fair presumption is that it is of high importance to that species: nevertheless it is in this case eminently liable to variation. Why should this be so? On the view that each species has been independently

created, with all its parts as we now see them, I can see no explanation. But on the view that groups of species are descended from some other species, and have been modified through natural selection, I think we can obtain some light. First let me make some preliminary remarks. If, in our domestic animals, any part or the whole animal be neglected, and no selection be applied, that part (for instance, the comb in the Dorking fowl) or the whole breed will cease to have a uniform character: and the breed may be said to be degenerating. In rudimentary organs, and in those which have been but little specialised for any particular purpose, and perhaps in polymorphic groups, we see a nearly parallel case; for in such cases natural selection either has not or cannot come into full play, and thus the organisation is left in a fluctuating condition. But what here more particularly concerns us is, that those points in our domestic animals, which at the present time are undergoing rapid change by continued selection, are also eminently liable to variation. Look at the individuals of the same breed of the pigeon; and see what a prodigious amount of difference there is in the beak of tumblers, in the beak and wattle of carriers, in the carriage and tail of fantails, &c., these being the points now mainly attended to by English fanciers. Even in the same sub-breed, as in that of the short-faced tumbler, it is notoriously difficult to breed nearly perfect birds, many departing widely from the standard. There may truly be said to be a constant struggle going on between, on the one hand, the tendency to reversion to a less perfect state, as well as an innate tendency to new variations, and, on the other hand, the power of steady selection to keep the breed true. In the long run selection gains the day, and we do not expect to fail so completely as to breed a bird as coarse as a common tumbler pigeon from a good short-faced strain. But as long as selection is rapidly going on, much variability in the parts undergoing modification may always be expected.

Now let us turn to nature. When a part has been developed in an extraordinary manner in any one species, compared with the other species of the same genus, we may conclude that this part has undergone an extraordinary amount of modification since the period when the several species branched off from the common progenitor of the genus. This period will seldom be remote in any extreme degree, as species rarely endure for more than one geological period. An extraordinary amount of modification implies an unusually large and long-continued amount of variability, which has continually been accumulated by natural selection for the benefit of the species. But as the variability of the extraordinarily developed part or organ has been so great and long-continued within a period not excessively remote, we might, as a general rule, still expect to find more variability in such parts than in other parts of the organisation which have remained for a much longer period nearly constant. And this, I am convinced, is the case. That the struggle between natural selection on the one hand, and the tendency to reversion and variability on the other hand, will in the course of time cease; and that the most abnormally developed organs may be made constant, I see no reason to doubt. Hence, when an organ, however abnormal it may be, has been transmitted in approximately the same condition to many modified descendants, as in the case of the wing of the bat, it must have existed, according to our theory, for an immense period in nearly the same state; and thus it has come not to be more variable than any other structure. It is only in those cases in which the modification has been comparatively recent and extraordinarily great that we ought to find the *generative variability*, as it may be called, still present in a high degree. For in this case the variability will seldom as yet have been fixed by the continued selection of the individuals varying in the required manner and degree, and by the continued rejection of those tending to revert to a former and less modified condition.

# Specific characters more variable than generic characters.

The principle discussed under the last heading may be applied to our present subject. It is notorious that specific characters are more variable than generic. To explain by a simple example what is meant: if in a large genus of plants some species had blue flowers and some had red, the colour would be only a specific character, and no one would be surprised at one of the blue species varying into red, or conversely; but if all the species had blue flowers, the colour would become a generic character, and its variation would be a more unusual circumstance. I have chosen this example because the explanation which most naturalists would advance is not here applicable, namely, that specific characters are more variable than generic, because they are taken from parts of less physiological importance than those commonly used for classing genera. I believe this explanation is partly, yet only indirectly, true; I shall, however, have to return to this point in the chapter on Classification. It would be almost superfluous to adduce evidence in support of the statement, that ordinary specific characters are more variable than generic; but with respect to important characters, I have repeatedly noticed in works on natural history, that when an author remarks with surprise that some important organ or part, which is generally very constant throughout a large group of species, *differs* considerably in closely-allied species, it is often *variable* in the individuals of the same species. And this fact shows that a character, which is generally of generic value, when it sinks in value and becomes only of specific value, often becomes variable, though its physiological importance may remain the same. Something of the same kind applies to monstrosities: at least Is. Geoffroy St. Hilaire apparently entertains no doubt, that the more an organ normally differs in the different species of the same group, the more subject it is to anomalies in the individuals.

On the ordinary view of each species having been independently created, why should that part of the structure, which differs from the same part in other independently created species of the same genus, be more variable than those parts which are closely alike in the several species? I do not see that any explanation can be given. But on the view that species are only strongly marked and fixed varieties, we might expect often to find them still continuing to vary in those parts of their structure which have varied within a moderately recent period, and which have thus come to differ. Or to state the case in another manner:— the points in which all the species of a genus resemble each other, and in which they differ from allied genera, are called generic characters; and these characters may be attributed to inheritance from a common progenitor, for it can rarely have happened that natural selection will have modified several distinct species, fitted to more or less widely different habits, in exactly the same manner: and as these so-called generic characters have been inherited from before the period when the several species first branched off from their common progenitor, and subsequently have not varied or come to differ in any degree, or only in a slight degree, it is not probable that they should vary at the present day. On the other hand, the points in which species differ from other species of the same genus are called specific characters; and as these specific characters have varied and come to differ since the period when the species branched off from a common progenitor, it is probable that they should still often be in some degree variable,— at least more variable than those parts of the organisation which have for a very long period remained constant.

*Secondary sexual characters variable.—*

I think it will be admitted by naturalists, without my entering on details, that secondary sexual characters are highly variable. It will also be admitted that species of the same group differ from each other more widely in their secondary sexual characters, than in other parts of their organisation; compare, for instance, the amount of difference between the males of gallinaceous birds, in which secondary sexual characters are strongly displayed, with the amount of difference between the females. The cause of the original variability of these characters is not manifest; but we can see why they should not have been rendered as constant and uniform as others, for they are accumulated by sexual selection, which is less rigid in its action than ordinary selection, as it does not entail death, but only gives fewer offspring to the less favoured males. Whatever the cause may be of the variability of secondary sexual characters, as they are highly variable, sexual selection will have had a wide scope for action, and may thus have succeeded in giving to the species of the same group a greater amount of difference in these than in other respects.

It is a remarkable fact, that the secondary differences between the two sexes of the same species are generally displayed in the very same parts of the organisation in which the species of the same genus differ from each other. Of this fact I will give in illustration the first two instances which happen to stand on my list; and as the differences in these cases are of a very unusual nature, the relation can hardly be accidental. The same number of joints in the tarsi is a character common to very large groups of beetles, but in the Engidæ, as Westwood has remarked, the number varies greatly and the number likewise differs in the two sexes of the same species. Again in the fossorial hymenoptera, the neuration of the wings is a character of the highest importance, because common to large groups; but in certain genera the neuration differs in the different species, and likewise in the two sexes of the same species. Sir J. Lubbock has recently remarked, that several minute crustaceans offer excellent illustrations of this law. "In *Pontella*, for instance, the sexual characters are afforded mainly by the anterior antennæ and by the fifth pair of legs: the specific differences also are principally given by these organs." This relation has a clear meaning on my view: I look at all the species of the same genus as having as certainly descended from the same progenitor, as have the two sexes of any one species. Consequently, whatever part of the structure of the common progenitor, or of its early descendants, became variable; variations of this part would, it is highly probable, be taken advantage of by natural and sexual selection, in order to fit the several places in the economy of nature, and likewise to fit the two sexes of the same species to each other, or to fit the males to struggle with other males for the possession of the females.

Finally, then, I conclude that the greater variability of specific characters, or those which distinguish species from species, than of generic characters, or those which are possessed by all the species; that the frequent extreme variability of any part which is developed in a species in an extraordinary manner in comparison with the same part in its congeners; and the slight degree of variability in a part, however extraordinarily it may be developed, if it be common to a whole group of species; that the great variability of secondary sexual characters and their great difference in closely allied species;— that secondary sexual and ordinary specific differences are generally displayed in the same parts of the organisation,— are all principles closely connected together. All being mainly due to the species of the same group being the descendants of a common progenitor, from whom they have inherited much in common,— to parts which have recently and largely varied being more likely still to go on varying than parts which have long been inherited and have not varied,— to natural selection having more or less completely, according to the lapse of time, overmastered the tendency to reversion and to further variability, to sexual selection being less rigid than ordinary selection, and to variations in the same parts having been accumulated by natural and sexual selection, and thus having been adapted for secondary sexual, and for ordinary purposes.

*Distinct Species present analogous Variations, so that a Variety of one Species often assumes a Character proper to an allied Species, or reverts to some of the Characters of an early Progenitor.—*

These propositions will be most readily understood by looking to our domestic races. The most distinct breeds of the pigeon, in countries widely apart, present sub-varieties with reversed feathers on the head, and with feathers on the feet,— characters not possessed by the aboriginal rock-pigeon; these then are analogous variations in two or more distinct races. The frequent presence of fourteen or even sixteen tail-feathers in the pouter may be considered as a variation representing the normal structure of another race, the fantail. I presume that no one will doubt that all such analogous variations are due to the several races of the pigeon having inherited from a common parent the same constitution and tendency to variation, when acted on by similar unknown influences. In the vegetable kingdom we have a case of analogous variation, in the enlarged stems, or as commonly called roots, of the Swedish turnip and ruta-baga, plants which several botanists rank as varieties produced by cultivation from a common parent: if this be not so, the case will then be one of analogous variation in two so-called distinct species; and to these a third may be added, namely, the common turnip. According to the ordinary view of each species having been independently created, we should have to attribute this similarity in the enlarged stems of these three plants, not to the *vera causa* of community of descent, and a consequent tendency to vary in a like manner, but to three separate yet closely related acts of creation. Many similar cases of analogous variation have been observed by Naudin in the great gourd family, and by various authors in our cereals. Similar cases occurring with insects under natural conditions have lately been discussed with much ability by Mr. Walsh, who has grouped them under his law of equable variability.

With pigeons, however, we have another case, namely, the occasional appearance in all the breeds, of slaty-blue birds with two black bars on the wings, white loins, a bar at the end of the tail, with the outer feathers externally edged near their bases with white. As all these marks are characteristic of the parent rock-pigeon, I presume that no one will doubt that this is a case of reversion, and not of a new yet analogous variation appearing in the several breeds. We may, I think, confidently come to this conclusion, because, as we have seen, these coloured marks are eminently liable to appear in the crossed offspring of two distinct and differently coloured breeds; and in this case there is nothing in the external conditions of life to cause the reappearance of the slaty-blue, with the several marks, beyond the influence of the mere act of crossing on the laws of inheritance.

No doubt it is a very surprising fact that characters should reappear after having been lost for many, probably for hundreds of generations. But when a breed has been crossed only once by some other breed, the offspring occasionally show for many generations a tendency to revert in character to the foreign breed — some say, for a dozen or even a score of generations. After twelve generations, the proportion of blood, to use a common expression, from one ancestor, is only 1 in 2048; and yet, as we see, it is generally believed that a tendency to reversion is retained by this remnant of foreign blood. In a breed which has not been crossed, but in which *both* parents have lost some character which their progenitor possessed, the tendency, whether strong or weak, to reproduce the lost character might, as was formerly remarked, for all that we can see to the contrary, be transmitted for almost any number of generations. When a character which has been lost in a breed, reappears after a great number of generations, the most probable hypothesis is, not that one individual suddenly takes after an ancestor removed by some hundred generations, but that in each successive generation the character in question has been lying latent, and at last, under unknown favourable conditions, is developed. With the barb-pigeon, for instance, which very rarely produces a blue bird, it is probable that there is a latent tendency in each generation to produce blue plumage. The abstract improbability of such a tendency

being transmitted through a vast number of generations, is not greater than that of quite useless or rudimentary organs being similarly transmitted. A mere tendency to produce a rudiment is indeed sometimes thus inherited.

As all the species of the same genus are supposed to be descended from a common progenitor, it might be expected that they would occasionally vary in an analogous manner; so that the varieties of two or more species would resemble each other, or that a variety of one species would resemble in certain characters another and distinct species,— this other species being, according to our view, only a well-marked and permanent variety. But characters exclusively due to analogous variation would probably be of an unimportant nature, for the preservation of all functionally important characters will have been determined through natural selection, in accordance with the different habits of the species. It might further be expected that the species of the same genus would occasionally exhibit reversion to long-lost characters. As, however, we do not know the common ancestor of any natural group, we cannot distinguish between reversionary and analogous characters. If, for instance, we did not know that the parent rock-pigeon was not feather-footed or turn-crowned, we could not have told, whether such characters in our domestic breeds were reversion to former characters or only analogous variations; but we might have inferred that the blue colour was a case of reversion from the number of the markings, which are correlated with this tint, and which would not probably have all appeared together from simple variation. More especially we might have inferred this from the blue colour and the several marks so often appearing when differently coloured breeds are crossed. Hence, although under nature it must generally be left doubtful, what cases are reversion to formerly existing characters, and what are new but analogous variations, yet we ought, on our theory, sometimes to find the varying offspring of a species assuming characters which are already present in other members of the same group. And this undoubtedly is the case.

The difficulty in distinguishing variable species is largely due to the varieties mocking, as it were, other species of the same genus. A considerable catalogue, also, could be given of forms intermediate between two other forms, which themselves can only doubtfully be ranked as species; and this shows, unless all these closely allied forms be considered as independently created species, that they have in varying assumed some of the characters of the others. But the best evidence of analogous variations is afforded by parts or organs which are generally constant in character, but which occasionally vary so as to resemble, in some degree, the same part or organ in an allied species. I have collected a long list of such cases; but here, as before, I lie under the great disadvantage of not being able to give them. I can only repeat that such cases certainly occur, and seem to me very remarkable.

I will, however, give one curious and complex case, not indeed as affecting any important character, but from occurring in several species of the same genus, partly under domestication and partly under nature. It is a case almost certainly of reversion. The ass sometimes has very distinct transverse bars on its legs, like those on the legs of a zebra. It has been asserted that these are plainest in the foal, and from inquiries which I have made, I believe this to be true. The stripe on the shoulder is sometimes double, and is very variable in length and outline. A white ass, but *not* an albino, has been described without either spinal or shoulder stripe; and these stripes are sometimes very obscure, or actually quite lost, in dark-coloured asses. The koulan of Pallas is said to have been seen with a double shoulder-stripe. Mr. Blyth has seen a specimen of the hemionus with a distinct shoulder-stripe, though it properly has none; and I have been informed by Colonel Poole that foals of this species are generally striped on the legs and faintly on the shoulder. The quagga, though so plainly barred like a zebra over the body, is without bars on the legs; but Dr. Gray has figured one specimen with very distinct zebra-like bars on the hocks.

With respect to the horse, I have collected cases in England of the spinal stripe in horses of the most distinct breeds, and of *all* colours; transverse bars on the legs are not rare in duns, mouse-duns, and in one instance in a chestnut; a faint shoulder-stripe may sometimes be seen in duns, and I have seen a trace in a bay horse. My son made a careful examination and sketch for me of a dun Belgian cart-horse with a double stripe on each shoulder and with leg-stripes. I have myself seen a dun Devonshire pony, and a small dun Welsh pony has been carefully described to me, both with *three* parallel stripes on each shoulder.

In the north-west part of India the Kattywar breed of horses is so generally striped, that, as I hear from Colonel Poole, who examined this breed for the Indian Government, a horse without stripes is not considered as purely bred. The spine is always striped; the legs are generally barred; and the shoulder-stripe, which is sometimes double and sometimes treble, is common; the side of the face, moreover, is sometimes striped. The stripes are often plainest in the foal; and sometimes quite disappear in old horses. Colonel Poole has seen both gray and bay Kattywar horses striped when first foaled. I have also reason to suspect, from information given me by Mr. W. W. Edwards, that with the English race-horse the spinal stripe is much commoner in the foal than in the full-grown animal. I have myself recently bred a foal from a bay mare (offspring of a Turkoman horse and a Flemish mare) by a bay English race-horse; this foal, when a week old, was marked on its hinder quarters and on its forehead with numerous very narrow, dark, zebra-like bars, and its legs were feebly striped. All the stripes soon disappeared completely. Without here entering on further details I may state that I have collected cases of leg and shoulder stripes in horses of very different breeds in various countries from Britain to Eastern China; and from Norway in the north to the Malay Archipelago in the south. In all parts of the world these stripes occur far oftenest in duns and mouse-duns; by the term dun a large range of colour is included, from one between brown and black to a close approach to cream-colour.

I am aware that Colonel Hamilton Smith, who has written on this subject, believes that the several breeds of the horse are descended from several aboriginal species — one of which, the dun, was striped; and that the above-described appearances are all due to ancient crosses with the dun stock. But this view may be safely rejected, for it is highly improbable that the heavy Belgian cart-horse, Welsh ponies, Norwegian cobs, the lanky Kattywar race, &c., inhabiting the most distant parts of the world, should have all have been crossed with one supposed aboriginal stock.

Now let us turn to the effects of crossing the several species of the horse-genus. Rollin asserts that the common mule from the ass and horse is particularly apt to have bars on its legs; according to Mr. Gosse, in certain parts of the United States, about nine out of ten mules have striped legs. I once saw a mule with its legs so much striped that any one might have thought that it was a hybrid zebra; and Mr. W. C. Martin, in his excellent treatise on the horse, has given a figure of a similar mule. In four coloured drawings, which I have seen, of hybrids between the ass and zebra, the legs were much more plainly barred than the rest of the body; and in one of them there was a double shoulder-stripe. In Lord Morton's famous hybrid, from a chestnut mare and male quagga, the hybrid and even the pure offspring subsequently produced from the same mare by a black Arabian sire, were much more plainly barred across the legs than is even the pure quagga. Lastly, and this is another most remarkable case, a hybrid has been figured by Dr. Gray (and he informs me that he knows of a second case) from the ass and the hemionus; and this hybrid, though the ass only occasionally has stripes on his legs and the hemionus has none and has not even a shoulder-stripe, nevertheless had all four legs barred, and had three short shoulder-stripes, like those on the dun Devonshire and Welsh ponies, and even had some zebra-like stripes on the sides of its face. With respect to this last fact, I was so convinced that not even a stripe of colour appears from what is commonly called chance, that I was led solely from the

occurrence of the face-stripes on this hybrid from the ass and hemionus to ask Colonel Poole whether such face-stripes ever occurred in the eminently striped Kattywar breed of horses, and was, as we have seen, answered in the affirmative.

What now are we to say to these several facts? We see several distinct species of the horse genus becoming, by simple variation, striped on the legs like a zebra, or striped on the shoulders like an ass. In the horse we see this tendency strong whenever a dun tint appears — a tint which approaches to that of the general colouring of the other species of the genus. The appearance of the stripes is not accompanied by any change of form, or by any other new character. We see this tendency to become striped most strongly displayed in hybrids from between several of the most distinct species. Now observe the case of the several breeds of pigeons: they are descended from a pigeon (including two or three sub-species or geographical races) of a bluish colour, with certain bars and other marks; and when any breed assumes by simple variation a bluish tint, these bars and other marks invariably reappear; but without any other change of form or character. When the oldest and truest breeds of various colours are crossed, we see a strong tendency for the blue tint and bars and marks to reappear in the mongrels. I have stated that the most probable hypothesis to account for the reappearance of very ancient characters, is — that there is a *tendency* in the young of each successive generation to produce the long-lost character, and that this tendency, from unknown causes, sometimes prevails. And we have just seen that in several species of the horse genus the stripes are either plainer or appear more commonly in the young than in the old. Call the breeds of pigeons, some of which have bred true for centuries, species; and how exactly parallel is the case with that of the species of the horse genus! For myself, I venture confidently to look back thousands on thousands of generations, and I see an animal striped like a zebra, but perhaps otherwise very differently constructed, the common parent of our domestic horse (whether or not it be descended from one or more wild stocks) of the ass, the hemionus, quagga, and zebra.

He who believes that each equine species was independently created, will, I presume, assert that each species has been created with a tendency to vary, both under nature and under domestication, in this particular manner, so as often to become striped like the other species of the genus; and that each has been created with a strong tendency, when crossed with species inhabiting distant quarters of the world, to produce hybrids resembling in their stripes, not their own parents, but other species of the genus. To admit this view is, as it seems to me, to reject a real for an unreal, or at least for an unknown cause. It makes the works of God a mere mockery and deception; I would almost as soon believe with the old and ignorant cosmogonists, that fossil shells had never lived, but had been created in stone so as to mock the shells now living on the sea-shore.

# Summary.

Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied. But whenever we have the means of instituting a comparison, the same laws appear to have acted in producing the lesser differences between varieties of the same species, and the greater differences between species of the same genus. Changed conditions generally induce mere fluctuating variability, but sometimes they cause direct and definite effects; and these may become strongly marked in the course of time, though we have not sufficient evidence on this head. Habit in producing constitutional peculiarities, and use in strengthening, and disuse in weakening and diminishing organs, appear in many cases to have been potent in their effects. Homologous parts tend to vary in the same manner, and homologous parts tend to cohere. Modifications in hard parts and in external parts sometimes affect softer and internal parts. When one part is largely developed, perhaps it tends to draw nourishment from the adjoining parts; and every part of the structure which can be saved without detriment will be saved. Changes of structure at an early age may affect parts subsequently developed; and many cases of correlated variation, the nature of which we are unable to understand, undoubtedly occur. Multiple parts are variable in number and in structure, perhaps arising from such parts not having been closely specialised for any particular function, so that their modifications have not been closely checked by natural selection. It follows probably from this same cause, that organic beings low in the scale are more variable than those standing higher in the scale, and which have their whole organisation more specialised. Rudimentary organs, from being useless, are not regulated by natural selection, and hence are variable. Specific characters — that is, the characters which have come to differ since the several species of the same genus branched off from a common parent — are more variable than generic characters, or those which have long been inherited, and have not differed within this same period. In these remarks we have referred to special parts or organs being still variable, because they have recently varied and thus come to differ; but we have also seen in the second chapter that the same principle applies to the whole individual; for in a district where many species of a genus are found — that is, where there has been much former variation and differentiation, or where the manufactory of new specific forms has been actively at work — in that district and among these species, we now find, on an average, most varieties. Secondary sexual characters are highly variable, and such characters differ much in the species of the same group. Variability in the same parts of the organisation has generally been taken advantage of in giving secondary sexual differences to the two sexes of the same species, and specific differences to the several species of the same genus. Any part or organ developed to an extraordinary size or in an extraordinary manner, in comparison with the same part or organ in the allied species, must have gone through an extraordinary amount of modification since the genus arose; and thus we can understand why it should often still be variable in a much higher degree than other parts; for variation is a long-continued and slow process, and natural selection will in such cases not as yet have had time to overcome the tendency to further variability and to reversion to a less modified state. But when a species with an extraordinarily developed organ has become the parent of many modified descendants — which on our view must be a very slow process, requiring a long lapse of time — in this case, natural selection has succeeded in giving a fixed character to the organ, in however extraordinary a manner it may have been developed. Species inheriting nearly the same constitution from a common parent, and exposed to similar influences, naturally tend to present analogous variations, or these same species may occasionally revert to some of the characters of their ancient progenitors. Although new and important modifications may not arise from reversion and analogous variation, such modifications will add to the beautiful and harmonious diversity of nature.

Whatever the cause may be of each slight difference between the offspring and their parents — and a cause for each must exist — we have reason to believe that it is the steady accumulation of beneficial differences which has given rise to all the more important modifications of structure in relation to the habits of each species.