CHAPTER XXII.

CAUSES OF VARIABILITY.

VARIABILITY DOES NOT NECESSARILY ACCOMPANY REPRODUCTION—CAUSES ASSIGNED BY VARIOUS AUTHORS—INDIVIDUAL DIFFERENCES—VARIABILITY OF EVERY KIND DUE TO CHANGED CONDITIONS OF LIFE—ON THE NATURE OF SUCH CHANGES — CLIMATE, FOOD, EXCESS OF NUTRIMENT — SLIGHT CHANGES SUFFICIENT—EFFECTS OF GRAFTING ON THE VARIABILITY OF SEEDLING-TREES — DOMESTIC PRODUCTIONS BECOME HABITUATED TO CHANGED CONDITIONS—ON THE ACCUMULATIVE ACTION OF CHANGED CONDITIONS—CLOSE INTERBREEDING AND THE IMAGINATION OF THE MOTHER SUPPOSED TO CAUSE VARIABILITY—CROSSING AS A CAUSE OF THE APPEARANCE OF NEW CHARACTERS—VARIABILITY FROM THE COMMINGLING OF CHARACTERS AND FROM REVERSION—ON THE MANNER AND PERIOD OF ACTION OF THE CAUSES WHICH EITHER DIRECTLY, OR INDIRECTLY THROUGH THE REPRODUCTIVE SYSTEM, INDUCE VARIABILITY.

WE will now consider, as far as we can, the causes of the almost universal variability of our domesticated productions. The subject is an obscure one; but it may be useful to probe our ignorance. Some authors, for instance Dr. Prosper Lucas, look at variability as a necessary contingent on reproduction, and as much an aboriginal law as growth or inheritance. Others have of late encouraged, perhaps unintentionally, this view by speaking of inheritance and variability as equal and antagonistic principles. Pallas maintained, and he has had some followers, that variability depends exclusively on the crossing of primordially distinct forms. Other authors attribute variability to an excess of food, and with animals to an excess relatively to the amount of exercise taken, or again to the effects of a more genial climate. That these causes are all effective is highly probable. But we must, I think, take a broader view, and conclude that organic beings, when subjected during several generations to any change whatever in their conditions, tend to vary; the kind of variation which ensues depending in most cases in a far higher degree on the nature or constitution of the being, than on the nature of the changed conditions.

Those authors who believe that it is a law of nature that each individual should differ in some slight degree from every other, may maintain, apparently with truth, that this is the fact, not only with all domesticated animals and cultivated plants, but likewise with all organic beings in a state of nature. The Laplander by long practice knows and gives a name to each reindeer, though, as Linnæus remarks, "to distinguish one from another among such multitudes was beyond my comprehension, for they were like ants on an ant-hill." In Germany shepherds have won wagers by recognising each sheep in a flock of a hundred, which they had never seen until the previous fortnight. This power of discrimination, however, is as nothing compared to that which some florists have acquired. Verlot mentions a gardener who could distinguish 150 kinds of camellia, when not in flower; and it has been positively asserted that the famous old Dutch florist Voorhelm, who kept above 1200 varieties of the hyacinth, was hardly ever deceived in knowing each variety by the bulb alone. Hence we must conclude that the bulbs of the hyacinth and the branches and leaves of the camellia, though appearing to an unpractised eye absolutely undistinguishable, yet really differ.[1]

As Linnæus has compared the reindeer in number to ants, I may add that each ant knows its fellow of the same community. Several times I carried ants of the same species (*Formica rufa*) from one ant-hill to another, inhabited apparently by tens of thousands of ants; but the strangers were instantly detected and killed. I then put some ants taken from a very large nest into a bottle strongly perfumed with assafœtida, and after an interval of twenty-four hours returned them to their home; they were at first threatened by their fellows, but were soon recognised and allowed to pass. Hence each ant certainly recognised, independently of odour, its fellow; and if all the ants of the same community have not some countersign or watchword, they must present to each other's senses some distinguishable character.

[1] 'Des Jacinthes,' &c., Amsterdam, 1768, p. 43; Verlot, 'Des Variétés,' &c., p. 86. On the reindeer, *see* Linnæus, 'Tour in Lapland,' translated by Sir J. E. Smith, vol. i. p. 314. The statement in regard to German shepherds is given on the authority of Dr. Weinland.

The dissimilarity of brothers or sisters of the same family, and of seedlings from the same capsule, may be in part accounted for by the unequal blending of the characters of the two parents, and by the more or less complete recovery through reversion of ancestral characters on either side; but we thus only push the difficulty further back in time, for what made the parents or their progenitors different? Hence the belief[2] that an innate tendency to vary exists, independently of external differences, seems at first sight probable. But even the seeds nurtured in the same capsule are not subjected to absolutely uniform conditions, as they draw their nourishment from different points; and we shall see in a future chapter that this difference sometimes suffices to affect the character of the future plant. The greater dissimilarity of the successive children of the same family in comparison with twins, which often resemble each other in external appearance, mental disposition, and constitution, in so extraordinary a manner, apparently proves that the state of the parents at the exact period of conception, or the nature of the subsequent embryonic development, has a direct and powerful influence on the character of the offspring. Nevertheless, when we

[2] Müller's 'Physiology,' Eng. translation, vol. ii. p. 1662. With respect to the similarity of twins in constitution, Dr. William Ogle has given me the following extract from Professor Trousseau's Lectures ('Clinique Médicale,' tom. i. p. 523), in which a curious case is recorded:—"J'ai donné mes soins à deux frères jumeaux, tous deux si extraordinairement ressemblants qu'il m'était impossible de les reconnaître, à moins de les voir l'un à côté de l'autre. Cette ressemblance physique s'étendait plus loin: ils avaient, permettez-moi l'expression, une similitude pathologique plus remarquable encore. Ainsi l'un d'eux que je voyais aux néothermes à Paris malade d'une ophthalmie rhumatismale me disait, 'En ce moment mon frère doit avoir une ophthalmie comme la mienne;' et comme je m'étais récrié, il me montrait quelques jours après une lettre qu'il venait de recevoir de ce frère alors à Vienne, et qui lui écrivait en effet—'J'ai mon ophthalmie, tu dois avoir la tienne.' Quelque singulier que ceci puisse paraître, le fait n'en est pas moins exact: on ne me l'a pas raconté, je l'ai vu, et j'en ai vu d'autres analogues dans ma pratique. Ces deux jumeaux étaient aussi tous deux asthmatiques, et asthmatiques à un effroyable degré. Originaires de Marseille, ils n'ont jamais pu demeurer dans cette ville, où leurs intérêts les appelaient souvent, sans être pris de leurs accès; jamais ils n'en éprouvaient à Paris. Bien mieux, il leur suffisait de gagner Toulon pour être guéris de leurs attaques de Marseille. Voyageant sans cesse et dans tous pays pour leurs affaires, ils avaient remarqué que certaines localités leur étaient funestes, que dans d'autres ils étaient exempts de tout phénomène d'oppression."

reflect on the individual differences between organic beings in a state of nature, as shown by every wild animal knowing its mate; and when we reflect on the infinite diversity of the many varieties of our domesticated productions, we may well be inclined to exclaim, though falsely as I believe, that Variability must be looked at as an ultimate fact, necessarily contingent on reproduction.

Those authors who adopt this latter view would probably deny that each separate variation has its own proper exciting cause. Although we can seldom trace the precise relation between cause and effect, yet the considerations presently to be given lead to the conclusion that each modification must have its own distinct cause, and is not the result of what we blindly call accident. The following striking case has been communicated to me by Dr. William Ogle. Two girls, born as twins, and in all respects extremely alike, had their little fingers on both hands crooked; and in both children the second bicuspid tooth of the second dentition, on the right side in the upper jaw was misplaced; for, instead of standing in a line with the others, it grew from the roof of the mouth behind the first bicuspid. Neither the parents nor any other members of the family were known to have exhibited any similar peculiarity; but a son of one of these girls had the same tooth similarly misplaced. Now, as both the girls were affected in exactly the same manner, the idea of accident is at once excluded: and we are compelled to admit that there must have existed some precise and sufficient cause which, if it had occurred a hundred times, would have given crooked fingers and misplaced bicuspid teeth to a hundred children. It is of course possible that this case may have been due to reversion to some long-forgotten progenitor, and this would much weaken the value of the argument. I have been led to think of the probability of reversion, from having been told by Mr. Galton of another case of twin girls born with their little fingers slightly crooked, which they inherited from their maternal grandmother.

We will now consider the general arguments, which appear to me to have great weight, in favour of the view that variations of all kinds and degrees are directly or indirectly caused

by the conditions of life to which each being, and more especially its ancestors, have been exposed.

No one doubts that domesticated productions are more variable than organic beings which have never been removed from their natural conditions. Monstrosities graduate so insensibly into mere variations that it is impossible to separate them; and all those who have studied monstrosities believe that they are far commoner with domesticated than with wild animals and plants;[3] and in the case of plants, monstrosities would be equally noticeable in the natural as in the cultivated state. Under nature, the individuals of the same species are exposed to nearly uniform conditions, for they are rigorously kept to their proper places by a host of competing animals and plants; they have, also, long been habituated to their conditions of life; but it cannot be said that they are subject to quite uniform conditions, and they are liable to a certain amount of variation. The circumstances under which our domestic productions are reared are widely different: they are protected from competition; they have not only been removed from their natural conditions and often from their native land, but they are frequently carried from district to district, where they are treated differently, so that they rarely remain during any considerable length of time exposed to closely similar conditions. In conformity with this, all our domesticated productions, with the rarest exceptions, vary far more than natural species. The hive-bee, which feeds itself and follows in most respects its natural habits of life, is the least variable of all domesticated animals, and probably the goose is the next least variable; but even the goose varies more than almost any wild bird, so that it cannot be affiliated with perfect certainty to any natural species. Hardly a single plant can be named, which has long been cultivated and propagated by seed, that is not highly variable; common rye (*Secale cereale*) has afforded fewer and less marked varieties than almost any other cultivated plant;[4] but it may be

[3] Isid. Geoffroy St.-Hilaire, 'Hist. des Anomalies,' tom. iii. p. 352; Moquin-Tandon, 'Tératologie Végétale,' 1841, p. 115.

[4] Metzger, 'Die Getreidearten,' 1841, s. 39.

doubted whether the variations of this, the least valuable of all our cereals, have been closely observed.

Bud-variation, which was fully discussed in a former chapter, shows us that variability may be quite independent of seminal reproduction, and likewise of reversion to long-lost ancestral characters. No one will maintain that the sudden appearance of a moss-rose on a Provence-rose is a return to a former state, for mossiness of the calyx has been observed in no natural species; the same argument is applicable to variegated and laciniated leaves; nor can the appearance of nectarines on peach-trees be accounted for on the principle of reversion. But bud-variations more immediately concern us, as they occur far more frequently on plants which have been highly cultivated during a length of time, than on other and less highly cultivated plants; and very few well-marked instances have been observed with plants growing under strictly natural conditions. I have given one instance of an ash-tree growing in a gentleman's pleasure-grounds; and occasionally there may be seen, on beech and other trees, twigs leafing at a different period from the other branches. But our forest trees in England can hardly be considered as living under strictly natural conditions; the seedlings are raised and protected in nursery-grounds, and must often be transplanted into places where wild trees of the kind would not naturally grow. It would be esteemed a prodigy if a dog-rose growing in a hedge produced by bud-variation a moss-rose, or a wild bullace or wild cherry-tree yielded a branch bearing fruit of a different shape and colour from the ordinary fruit. The prodigy would be enhanced if these varying branches were found capable of propagation, not only by grafts, but sometimes by seed; yet analogous cases have occurred with many of our highly cultivated trees and herbs.

These several considerations alone render it probable that variability of every kind is directly or indirectly caused by changed conditions of life. Or, to put the case under another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability.

On the Nature of the Changes in the Conditions of Life which induce Variability.

From a remote period to the present day, under climates and circumstances as different as it is possible to conceive, organic beings of all kinds, when domesticated or cultivated, have varied. We see this with the many domestic races of quadrupeds and birds belonging to different orders, with gold-fish and silkworms, with plants of many kinds, raised in various quarters of the world. In the deserts of northern Africa the date-palm has yielded thirty-eight varieties; in the fertile plains of India it is notorious how many varieties of rice and of a host of other plants exist; in a single Polynesian island, twenty-four varieties of the bread-fruit, the same number of the banana, and twenty-two varieties of the arum, are cultivated by the natives; the mulberry-tree in India and Europe has yielded many varieties serving as food for the silkworm; and in China sixty-three varieties of the bamboo are used for various domestic purposes.[5] These facts, and innumerable others which could be added, indicate that a change of almost any kind in the conditions of life suffices to cause variability—different changes acting on different organisms.

Andrew Knight[6] attributed the variation of both animals and plants to a more abundant supply of nourishment, or to a more favourable climate, than that natural to the species. A more genial climate, however, is far from necessary; the kidney-bean, which is often injured by our spring frosts, and peaches, which require the protection of a wall, have varied much in England, as has the orange-tree in northern Italy, where it is barely able to exist.[7] Nor can we overlook the

[5] On the date-palm, *see* Vogel, 'Annals and Mag. of Nat. Hist.,' 1854, p. 460. On Indian varieties, Dr. F. Hamilton, 'Transact. Linn. Soc.,' vol. xiv. p. 296. On the varieties cultivated in Tahiti, *see* Dr. Bennett, in Loudon's 'Mag. of N. Hist.,' vol. v., 1832, p. 484. Also Ellis, 'Polynesian Researches,' vol. i. pp. 370, 375. On twenty varieties of the Pandanus and other trees in the Marianne Island, *see* 'Hooker's Miscellany,' vol. i. p. 308. On the bamboo in China, *see* Huc's 'Chinese Empire,' vol. ii. p. 307.

[6] 'Treatise on the Culture of the Apple,' &c., p. 3.

[7] Gallesio, 'Teoria della Riproduzione Veg.,' p. 125.

fact, though not immediately connected with our present subject, that the plants and shells of the Arctic regions are eminently variable.[8] Moreover, it does not appear that a change of climate, whether more or less genial, is one of the most potent causes of variability; for in regard to plants Alph. De Candolle, in his 'Géographie Botanique,' repeatedly shows that the native country of a plant, where in most cases it has been longest cultivated, is that where it has yielded the greatest number of varieties.

It is doubtful whether a change in the nature of the food is a potent cause of variability. Scarcely any domesticated animal has varied more than the pigeon or the fowl, but their food, especially that of highly-bred pigeons, is generally the same. Nor can our cattle and sheep have been subjected to any great change in this respect. But in all these cases the food probably is much less varied in kind than that which was consumed by the species in its natural state.[9]

Of all the causes which induce variability, excess of food, whether or not changed in nature, is probably the most powerful. This view was held with regard to plants by Andrew Knight, and is now held by Schleiden, more especially in reference to the inorganic elements of the food.[10] In order to give a plant more food it suffices in most cases to grow it separately, and thus prevent other plants robbing its roots. It is surprising, as I have often seen, how vigorously our common wild species flourish when planted by themselves, though not in highly manured land; separate growth is, in fact, the first step in cultivation. We see the converse of the belief that excess of food induces variability in the following statement by a great raiser of seeds of all kinds:[11]

[8] *See* Dr. Hooker's Memoir on Arctic Plants in 'Linn. Transact.,' vol. xxiii. part ii. Mr. Woodward, and a higher authority cannot be quoted, speaks of the Arctic mollusca (in his 'Rudimentary Treatise,' 1856, p. 355) as remarkably subject to variation.

[9] Bechstein, in his 'Naturgeschichte der Stubenvögel,' 1840, s. 238, has some good remarks on this subject. He states that his canary-birds varied in colour, though kept on uniform food.

[10] 'The Plant,' by Schleiden, translated by Henfrey, 1848, p. 169. *See* also Alex. Braun, in 'Bot. Memoirs,' Ray Soc., 1853, p. 313.

[11] Messrs. Hardy and Son, of Maldon, in 'Gard. Chronicle,' 1856, p. 458. Carrière, 'Production et Fixation des Variétés,' 1865, p. 31.

"It is a rule invariably with us, when we desire to keep a "true stock of any one kind of seed, to grow it on poor land "without dung; but when we grow for quantity, we act "contrary, and sometimes have dearly to repent of it." According also to Carrière, who has had great experience with flower-garden seeds, "On remarque en général les plantes de "vigeur moyenne sont celles qui conservent le mieux leurs "caractères."

In the case of animals the want of a proper amount of exercise, as Bechstein remarked, has perhaps played, independently of the direct effects of the disuse of any particular organ, an important part in causing variability. We can see in a vague manner that, when the organised and nutrient fluids of the body are not used during growth, or by the wear and tear of the tissues, they will be in excess; and as growth, nutrition, and reproduction are intimately allied processes, this superfluity might disturb the due and proper action of the reproductive organs, and consequently affect the character of the future offspring. But it may be argued that neither an excess of food nor a superfluity in the organised fluids of the body necessarily induces variability. The goose and the turkey have been well fed for many generations, yet have varied very little. Our fruit-trees and culinary plants, which are so variable, have been cultivated from an ancient period, and, though they probably still receive more nutriment than in their natural state, yet they must have received during many generations nearly the same amount; and it might be thought that they would have become habituated to the excess. Nevertheless, on the whole, Knight's view, that excess of food is one of the most potent causes of variability, appears, as far as I can judge, probable.

Whether or not our various cultivated plants have received nutriment in excess, all have been exposed to changes of various kinds. Fruit-trees are grafted on different stocks, and grown in various soils. The seeds of culinary and agricultural plants are carried from place to place; and during the last century the rotation of our crops and the manures used have been greatly changed.

Slight changes of treatment often suffice to induce varia-

bility. The simple fact of almost all our cultivated plants and domesticated animals having varied in all places and at all times, leads to this conclusion. Seeds taken from common English forest-trees, grown under their native climate, not highly manured or otherwise artificially treated, yield seedlings which vary much, as may be seen in every extensive seed-bed. I have shown in a former chapter what a number of well-marked and singular varieties the thorn (*Cratægus oxycantha*) has produced: yet this tree has been subjected to hardly any cultivation. In Staffordshire I carefully examined a large number of two British plants, namely *Geranium phœum* and *pyrenaicum*, which have never been highly cultivated. These plants had spread spontaneously by seed from a common garden into an open plantation; and the seedlings varied in almost every single character, both in their flower and foliage, to a degree which I have never seen exceeded; yet they could not have been exposed to any great change in their conditions.

With respect to animals, Azara has remarked with much surprise,[12] that, whilst the feral horses on the Pampas are always of one of three colours, and the cattle always of a uniform colour, yet these animals, when bred on the unenclosed estancias, though kept in a state which can hardly be called domesticated, and apparently exposed to almost identically the same conditions as when they are feral, nevertheless display a great diversity of colour. So again in India several species of fresh-water fish are only so far treated artificially, that they are reared in great tanks; but this small change is sufficient to induce much variability.[13]

Some facts on the effects of grafting, in regard to the variability of trees, deserve attention. Cabanis asserts that when certain pears are grafted on the quince, their seeds yield a greater number of varieties than do the seeds of the same variety of pear when grafted on the wild pear.[14] But as the pear and quince are distinct species, though so closely related

[12] 'Quadrupèdes du Paraguay,' 1801, tom. ii. p. 319.

[13] M'Clelland on Indian Cyprinidæ, 'Asiatic Researches,' vol. xix. part ii., 1839, pp. 266, 268, 313.

[14] Quoted by Sageret, 'Pom. Phys., 1830, p. 43. This statement, however, is not believed by Decaisne.

that the one can be readily grafted and succeeds admirably on the other, the fact of variability being thus caused is not surprising; as we are here enabled to see the cause, namely, the very different nature of the stock and graft. Several North American varieties of the plum and peach are well known to reproduce themselves truly by seed; but Downing asserts,[15] "that when a graft is taken from one of these trees and "placed upon another stock, this grafted tree is found to lose "its singular property of producing the same variety by "seed, and becomes like all other worked trees;"—that is, its seedlings become highly variable. Another case is worth giving: the Lalande variety of the walnut-tree leafs between April 20th and May 15th, and its seedlings invariably inherit the same habit; whilst several other varieties of the walnut leaf in June. Now, if seedlings are raised from the May-leafing Lalande variety, grafted on another May-leafing variety, though both stock and graft have the same early habit of leafing, yet the seedlings leaf at various times, even as late as the 5th of June.[16] Such facts as these are well fitted to show on what obscure and slight causes variability depends.

I may here just allude to the appearance of new and valuable varieties of fruit-trees and of wheat in woods and waste places, which at first sight seems a most anomalous circumstance. In France a considerable number of the best pears have been discovered in woods; and this has occurred so frequently, that Piteau asserts that "improved varieties of our cultivated fruits rarely originate with nurserymen.[17] In England, on the other hand, no instance of a good pear having been found wild has been recorded; and Mr. Rivers informs me that he knows of only one instance with apples, namely, the Bess Poole, which was discovered in a wood in Nottinghamshire. This difference between the two countries may be in part accounted for by the more favourable climate of France, but chiefly

[15] 'The Fruits of America,' 1845, p. 5.

[16] M. Cardan, in 'Comptes Rendus,' Dec. 1848, quoted in 'Gard. Chronicle,' 1849, p. 101.

[17] M. Alexis Jordan mentions four excellent pears found in woods in France, and alludes to others ('Mém. Acad. de Lyon,' tom. ii. 1852, p. 159). Poiteau's remark is quoted in 'Gardener's Mag.,' vol. iv., 1828, p. 385. *See* 'Gard. Chronicle,' 1862, p. 335, for another case of a new variety of the pear found in a hedge in France. Also for another case, *see* Loudon's 'Encyclop. of Gardening,' p. 901. Mr. Rivers has given me similar information.

from the great number of seedlings which spring up there in the woods. I infer that this is the case from a remark made by a French gardener,[18] who regards it as a national calamity that such a number of pear-trees are periodically cut down for firewood, before they have borne fruit. The new varieties which thus spring up in the woods, though they cannot have received any excess of nutriment, will have been exposed to abruptly changed conditions, but whether this is the cause of their production is very doubtful. These varieties, however, are probably all descended[19] from old cultivated kinds growing in adjoining orchards,—a circumstance which will account for their variability; and out of a vast number of varying trees there will always be a good chance of the appearance of a valuable kind. In North America, where fruit-trees frequently spring up in waste places, the Washington pear was found in a hedge, and the Emperor peach in a wood.[20]

With respect to wheat, some writers have spoken[21] as if it were an ordinary event for new varieties to be found in waste places; the Fenton wheat was certainly discovered growing on a pile of basaltic detritus in a quarry, but in such a situation the plant would probably receive a sufficient amount of nutriment. The Chidham wheat was raised from an ear found *on* a hedge; and Hunter's wheat was discovered *by* the roadside in Scotland, but it is not said that this latter variety grew where it was found.[22]

Whether our domestic productions would ever become so completely habituated to the conditions under which they now live, as to cease varying, we have no sufficient means for judging. But, in fact, our domestic productions are never exposed for a great length of time to uniform conditions, and it is certain that our most anciently cultivated plants, as well as animals, still go on varying, for all have recently undergone marked improvement. In some few cases, however, plants have become habituated to new conditions. Thus, Metzger, who cultivated in Germany during many years numerous varieties of wheat, brought from different countries,[23] states that some kinds were at first extremely variable, but gradually, in one instance after an interval of

[18] Duval, 'Hist. du Poirier,' 1849, p. 2.

[19] I infer that this is the fact from Van Mons' statement ('Arbres Fruitiers,' 1835, tom. i. p. 446) that he finds in the woods seedlings resembling all the chief cultivated races of both the pear and apple. Van Mons, however looked at these wild varieties as aboriginal species.

[20] Downing, 'Fruit-trees of North America,' p. 422; Foley, in 'Transact. Hort. Soc.,' vol. vi. p. 412.

[21] 'Gard. Chronicle,' 1847, p. 244.

[22] 'Gardener's Chronicle,' 1841, p. 383; 1850, p. 700; 1854, p. 650.

[23] 'Die Getreidearten,' 1843, s. 66, 116, 117.

twenty-five years, became constant; and it does not appear that this resulted from the selection of the more constant forms.

On the Accumulative Action of changed Conditions of Life.— We have good grounds for believing that the influence of changed conditions accumulates, so that no effect is produced on a species until it has been exposed during several generations to continued cultivation or domestication. Universal experience shows us that when new flowers are first introduced into our gardens they do not vary; but ultimately all, with the rarest exceptions, vary to a greater or less extent. In a few cases the requisite number of generations, as well as the successive steps in the progress of variation, have been recorded, as in the often quoted instance of the Dahlia.[24] After several years' culture the Zinnia has only lately (1860) begun to vary in any great degree. "In the first seven or "eight years of high cultivation, the Swan River daisy "(*Brachycome iberidifolia*) kept to its original colour; it then "varied into lilac and purple and other minor shades."[25] Analogous facts have been recorded with the Scotch rose. In discussing the variability of plants several experienced horticulturists have spoken to the same general effect. Mr. Salter[26] remarks, "Every one knows that the chief difficulty "is in breaking through the original form and colour of the "species, and every one will be on the look-out for any "natural sport, either from seed or branch; that being once "obtained, however trifling the change may be, the result "depends upon himself." M. de Jonghe, who has had so much success in raising new varieties of pears and strawberries,[27] remarks with respect to the former, "There is another prin- "ciple, namely, that the more a type has entered into a state "of variation, the greater is its tendency to continue doing "so; and the more it has varied from the original type, the

[24] Sabine, in 'Hort. Transact.,' vol. iii. p. 225; Bronn, 'Geschichte der Natur,' b. ii. s. 119.

[25] 'Journal of Horticulture,' 1861, p. 112; on Zinnia, 'Gardener's Chronicle,' 1860, p. 852.

[26] 'The Chrysanthemum, its History, &c.,' 1865, p. 3.

[27] 'Gardener's Chron.,' 1855, p. 54; 'Journal of Horticulture,' May 9, 1865, p. 363.

"more it is disposed to vary still farther." We have, indeed, already discussed this latter point when treating of the power which man possesses, through selection, of continually augmenting in the same direction each modification; for this power depends on continued variability of the same general kind. The most celebrated horticulturist in France, namely, Vilmorin,[28] even maintains that, when any particular variation is desired, the first step is to get the plant to vary in any manner whatever, and to go on selecting the most variable individuals, even though they vary in the wrong direction; for the fixed character of the species being once broken, the desired variation will sooner or later appear.

As nearly all our animals were domesticated at an extremely remote epoch, we cannot, of course, say whether they varied quickly or slowly when first subjected to new conditions. But Dr. Bachman[29] states that he has seen turkeys raised from the eggs of the wild species lose their metallic tints and become spotted with white in the third generation. Mr. Yarrell many years ago informed me that the wild ducks bred on the ponds in St. James's Park, which had never been crossed, as it is believed, with domestic ducks, lost their true plumage after a few generations. An excellent observer,[30] who has often reared ducks from the eggs of the wild bird, and who took precautions that there should be no crossing with domestic breeds, has given, as previously stated, full details on the changes which they gradually undergo. He found that he could not breed these wild ducks true for more than five or six generations, "as they then proved so much "less beautiful. The white collar round the neck of the "mallard became much broader and more irregular, and "white feathers appeared in the ducklings' wings." They increased also in size of body; their legs became less fine, and they lost their elegant carriage. Fresh eggs were then procured from wild birds; but again the same result followed. In these cases of the duck and turkey we see that animals,

[28] Quoted by Verlot, 'Des Variétés,' &c., 1865, p. 28.

[29] 'Examination of the Characteristics of Genera and Species:' Charleston, 1855, p. 14.

[30] Mr. Hewitt, 'Journal of Hort.,' 1863, p. 39.

like plants, do not depart from their primitive type until they have been subjected during several generations to domestication. On the other hand, Mr. Yarrell informed me that the Australian dingos, bred in the Zoological Gardens, almost invariably produced in the first generation puppies marked with white and other colours; but these introduced dingos had probably been procured from the natives, who keep them in a semi-domesticated state. It is certainly a remarkable fact that changed conditions should at first produce, as far as we can see, absolutely no effect; but that they should subsequently cause the character of the species to change. In the chapter on pangenesis I shall attempt to throw a little light on this fact.

Returning now to the causes which are supposed to induce variability. Some authors[31] believe that close interbreeding gives this tendency, and leads to the production of monstrosities. In the seventeenth chapter some few facts were advanced, showing that monstrosities are, as it appears, occasionally thus induced; and there can be no doubt that close interbreeding causes lessened fertility and a weakened constitution; hence it may lead to variability: but I have not sufficient evidence on this head. On the other hand, close interbreeding, if not carried to an injurious extreme, far from causing variability, tends to fix the character of each breed.

It was formerly a common belief, still held by some persons, that the imagination of the mother affects the child in the womb.[32] This view is evidently not applicable to the lower animals, which lay unimpregnated eggs, or to plants. Dr. William Hunter, in the last century, told my father that during many years every woman in a large London Lying-in Hospital was asked before her confinement whether anything had specially affected her mind, and the answer was written down; and it so happened that in no one instance could a coincidence be detected between the woman's answer and any

[31] Devay, 'Mariages Consanguins,' pp. 97, 125. In conversation I have found two or three naturalists of the same opinion.

[32] Müller has conclusively argued against this belief, 'Elements of Phys.,' Eng. translat., vol. ii. 1842, p. 1405.

abnormal structure; but when she knew the nature of the structure, she frequently suggested some fresh cause. The belief in the power of the mother's imagination may perhaps have arisen from the children of a second marriage resembling the previous father, as certainly sometimes occurs, in accordance with the facts given in the eleventh chapter.

Crossing as a Cause of Variability.—In an early part of this chapter it was stated that Pallas[33] and a few other naturalists maintain that variability is wholly due to crossing. If this means that new characters never spontaneously appear in our domestic races, but that they are all directly derived from certain aboriginal species, the doctrine is little less than absurd; for it implies that animals like Italian greyhounds, pug-dogs, bull-dogs, pouter and fantail pigeons, &c., were able to exist in a state of nature. But the doctrine may mean something widely different, namely, that the crossing of distinct species is the sole cause of the first appearance of new characters, and that without this aid man could not have formed his various breeds. As, however, new characters have appeared in certain cases by bud-variation, we may conclude with certainty that crossing is not necessary for variability. It is, moreover, certain that the breeds of various animals, such as of the rabbit, pigeon, duck, &c., and the varieties of several plants, are the modified descendants of a single wild species. Nevertheless, it is probable that the crossing of two forms, when one or both have long been domesticated or cultivated, adds to the variability of the offspring, independently of the commingling of the characters derived from the two parent-forms; and this implies that new characters actually arise. But we must not forget the facts advanced in the thirteenth chapter, which clearly prove that the act of crossing often leads to the reappearance or reversion of long-lost characters; and in most cases it would be impossible to distinguish between the reappearance of ancient characters and the first appearance of absolutely new characters. Practically, whether new or old, they would be new to the breed in which they reappeared.

[33] 'Act. Acad. St. Petersburg,' 1780, part ii. p. 84, &c.

Gärtner declares,[34] and his experience is of the highest value on such a point, that, when he crossed native plants which had not been cultivated, he never once saw in the offspring any new character; but that from the odd manner in which the characters derived from the parents were combined, they sometimes appeared as if new. When, on the other hand, he crossed cultivated plants, he admits that new characters occasionally appeared, but he is strongly inclined to attribute their appearance to ordinary variability, not in any way to the cross. An opposite conclusion, however, appears to me the more probable. According to Kölreuter, hybrids in the genus Mirabilis vary almost infinitely, and he describes new and singular characters in the form of the seeds, in the colour of the anthers, in the cotyledons being of immense size, in new and highly peculiar odours, in the flowers expanding early in the season, and in their closing at night. With respect to one lot of these hybrids, he remarks that they presented characters exactly the reverse of what might have been expected from their parentage.[35]

Prof. Lecoq[36] speaks strongly to the same effect in regard to this same genus, and asserts that many of the hybrids from *Mirabilis jalapa* and *multiflora* might easily be mistaken for distinct species, and adds that they differed in a greater degree than the other species of the genus, from *M. jalapa*. Herbert, also, has described[37] certain hybrid Rhododendrons as being "as *unlike all others* in "foliage, as if they had been a separate species." The common experience of floriculturists proves that the crossing and recrossing of distinct but allied plants, such as the species of Petunia, Calceolaria, Fuchsia, Verbena, &c., induces excessive variability; hence the appearance of quite new characters is probable. M. Carrière[38] has lately discussed this subject: he states that *Erythrina cristagalli* had been multiplied by seed for many years, but had not yielded any varieties: it was then crossed with the allied *E. herbacea*, and "the resistance was now overcome, and varieties were produced "with flowers of extremely different size, form, and colour."

From the general and apparently well-founded belief that the crossing of distinct species, besides commingling their characters, adds greatly to their variability, it has probably arisen that some botanists have gone so far as to maintain[39] that, when a genus includes only a single species, this when cultivated never varies. The proposition made so broadly cannot be admitted; but it is probably true that the variability of monotypic genera when culti-

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[34] 'Bastarderzeugung,' s. 249, 255, 295.

[35] 'Nova Acta, St. Petersburg,' 1794, p. 378; 1795, pp. 307, 313, 316; 1787, p. 407.

[36] 'De la Fécondation,' 1862, p. 311.

[37] 'Amaryllidaceæ,' 1837, p. 362.

[38] Abstracted in 'Gard. Chronicle,' 1860, p. 1081.

[39] This was the opinion of the elder De Candolle, as quoted in 'Dic. Class. d'Hist. Nat.,' tom. viii. p. 405. Puvis, in his work, 'De la Dégénération,' 1837, p. 37, has discussed this same point.

vated is generally less than that of genera including numerous species, and this quite independently of the effects of crossing. I have shown in my 'Origin of Species,' that the species belonging to small genera generally yield a less number of varieties in a state of nature than those belonging to large genera. Hence the species of small genera would, it is probable, produce fewer varieties under cultivation than the already variable species of larger genera.

Although we have not at present sufficient evidence that the crossing of species, which have never been cultivated, leads to the appearance of new characters, this apparently does occur with species which have been already rendered in some degree variable through cultivation. Hence crossing, like any other change in the conditions of life, seems to be an element, probably a potent one, in causing variability. But we seldom have the means of distinguishing, as previously remarked, between the appearance of really new characters and the reappearance of long-lost characters, evoked through the act of crossing. I will give an instance of the difficulty in distinguishing such cases. The species of Datura may be divided into two sections, those having white flowers with green stems, and those having purple flowers with brown stems: now Naudin[40] crossed *Datura lævis* and *ferox*, both of which belong to the white section, and raised from them 205 hybrids. Of these hybrids, every one had brown stems and bore purple flowers; so that they resembled the species of the other section of the genus, and not their own two parents. Naudin was so much astonished at this fact, that he was led carefully to observe both parent-species, and he discovered that the pure seedlings of *D. ferox*, immediately after germination, had dark purple stems, extending from the young roots up to the cotyledons, and that this tint remained ever afterwards as a ring round the base of the stem of the plant when old. Now I have shown in the thirteenth chapter that the retention or exaggeration of an early character is so intimately related to reversion, that it evidently comes under the same principle. Hence probably we ought to look at the purple flowers and brown stems of these hybrids, not as new characters due to variability, but as a return to the former state of some ancient progenitor.

Independently of the appearance of new characters from crossing, a few words may be added to what has been said in former chapters on the unequal combination and transmission of the characters proper to the two parent-forms. When two species or races are crossed, the offspring of the first generation are generally uniform, but those subsequently produced display an almost infinite diversity of character. He who wishes, says Kölreuter,[41] to obtain an endless number of varieties from hybrids should cross and recross them. There is also much variability when hybrids or mongrels are reduced or absorbed by repeated crosses with either pure parent-

[40] 'Comptes Rendus,' Novembre 21, 1864, p. 838.

[41] 'Nova Acta, St. Petersburg, 1794, p. 391.

form: and a still higher degree of variability when three distinct species, and most of all when four species, are blended together by successive crosses. Beyond this point Gärtner,[42] on whose authority the foregoing statements are made, never succeeded in effecting a union; but Max Wichura[43] united six distinct species of willows into a single hybrid. The sex of the parent species affects in an inexplicable manner the degree of variability of hybrids; for Gärtner[44] repeatedly found that when a hybrid was used as a father and either one of the pure parent-species, or a third species, was used as the mother, the offspring were more variable than when the same hybrid was used as the mother, and either pure parent or the same third species as the father: thus seedlings from *Dianthus barbatus* crossed by the hybrid *D. chinensi-barbatus* were more variable than those raised from this latter hybrid fertilised by the pure *D. barbatus*. Max Wichura[45] insists strongly on an analogous result with his hybrid willows. Again Gärtner[46] asserts that the degree of variability sometimes differs in hybrids raised from reciprocal crosses between the same two species; and here the sole difference is, that the one species is first used as the father and then as the mother. On the whole we see that, independently of the appearance of new characters, the variability of successive crossed generations is extremely complex, partly from the offspring partaking unequally of the characters of the two parent-forms, and more especially from their unequal tendency to revert to such characters or to those of more ancient progenitors.

On the Manner and on the Period of Action of the Causes which induce Variability.—This is an extremely obscure subject, and we need here only consider, whether inherited variations are due to certain parts being acted on after they have been formed, or through the reproductive system being affected before their formation; and in the former case at what period of growth or development the effect is produced. We shall see in the two following chapters that various agencies, such as an abundant supply of food, exposure to a different climate, increased use or disuse of parts, &c., prolonged during several generations, certainly modify either the whole organisation or certain organs; and it is clear at least in the case of bud-variation that the action cannot have been through the reproductive system.

[42] 'Bastarderzeugung,' s. 507, 516, 572.

[43] 'Die Bastardbefruchtung,' &c., 1865, s. 24.

[44] 'Bastarderzeugung,' s. 452, 507

[45] 'Die Bastardbefruchtung,' s. 56.

[46] 'Bastarderzeugung,' s. 423.

With respect to the part which the reproductive system takes in causing variability, we have seen in the eighteenth chapter that even slight changes in the conditions of life have a remarkable power in causing a greater or less degree of sterility. Hence it seems not improbable that beings generated through a system so easily affected should themselves be affected, or should fail to inherit, or inherit in excess, characters proper to their parents. We know that certain groups of organic beings, but with exceptions in each group, have their reproductive systems much more easily affected by changed conditions than other groups; for instance, carnivorous birds more readily than carnivorous mammals, and parrots more readily than pigeons; and this fact harmonises with the apparently capricious manner and degree in which various groups of animals and plants vary under domestication.

Kölreuter[47] was struck with the parallelism between the excessive variability of hybrids when crossed and recrossed in various ways,—these hybrids having their reproductive powers more or less affected,—and the variability of anciently cultivated plants. Max Wichura[48] has gone one step farther, and shows that with many of our highly cultivated plants, such as the hyacinth, tulip, auricula, snapdragon, potato, cabbage, &c., which there is no reason to believe have been hybridised, the anthers contain many irregular pollen-grains in the same state as in hybrids. He finds also in certain wild forms, the same coincidence between the state of the pollen and a high degree of variability, as in many species of Rubus; but in *R. cæsius* and *idæus*, which are not highly variable species, the pollen is sound. It is also notorious that many cultivated plants, such as the banana, pine-apple, bread-fruit, and others previously mentioned, have their reproductive organs so seriously affected as to be generally quite sterile; and when they do yield seed, the seedlings, judging from the large number of cultivated races which exist, must be variable in an extreme degree. These facts indicate that there is some relation between the state of the reproductive organs and a tendency to variability; but we must not conclude that the relation is strict. Although many of our highly cultivated plants may have their pollen in a deteriorated condition, yet, as we have previously seen, they yield more seeds, and our anciently domesticated animals are more prolific, than the corresponding species in a state of nature. The peacock is almost the only bird which is believed to be less fertile under domestication than in its native state, and it has varied in a remarkably small degree. From these considerations it would seem that changes in the conditions of life lead either to sterility or to variability, or to both; and not that sterility induces variability. On the whole it is probable that any cause affecting the organs of

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[47] 'Dritte Fortsetzung,' &c., 1766, s. 85.

[48] 'Die Bastardbefruchtung,' &c., 1865, s. 92: *see* also the Rev. M. J. Berkeley on the same subject, in 'Journal of Royal Hort. Soc.,' 1866, p. 80.

reproduction would likewise affect their product,—that is, the offspring thus generated.

The period of life at which the causes that induce variability act, is likewise an obscure subject, which has been discussed by various authors.[49] In some of the cases, to be given in the following chapter, of modifications from the direct action of changed conditions, which are inherited, there can be no doubt that the causes have acted on the mature or nearly mature animal. On the other hand, monstrosities, which cannot be distinctly separated from lesser variations, are often caused by the embryo being injured whilst in the mother's womb or in the egg. Thus I. Geoffroy Saint-Hilaire[50] asserts that poor women who work hard during their pregnancy, and the mothers of illegitimate children troubled in their minds and forced to conceal their state, are far more liable to give birth to monsters than women in easy circumstances. The eggs of the fowl when placed upright or otherwise treated unnaturally frequently produce monstrous chickens. It would, however, appear that complex monstrosities are induced more frequently during a rather late than during a very early period of embryonic life; but this may partly result from some one part, which has been injured during an early period, affecting by its abnormal growth other parts subsequently developed; and this would be less likely to occur with parts injured at a later period.[51] When any part or organ becomes monstrous through abortion, a rudiment is generally left, and this likewise indicates that its development had already commenced.

Insects sometimes have their antennæ or legs in a monstrous condition, the larvæ of which do not possess either antennæ or legs; and in these cases, as Quatrefages[52] believes, we are enabled to see the precise period at which the normal progress of development was troubled. But the nature of the food given to a caterpillar sometimes affects the colours of the moth, without the caterpillar itself being affected; therefore it seems possible that other characters in the mature insect might be indirectly modified through the larvæ. There is no reason to suppose that organs which have been rendered monstrous have always been acted on during their development; the cause may have acted on the organisation at a much earlier stage. It is even probable that either the male or female sexual elements, or both, before their union, may be affected in such a manner as to lead to modifications in organs developed at a late period of life; in nearly the same manner as a child may inherit from his father a disease which does not appear until old age.

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[49] Dr. P. Lucas has given a history of opinion on this subject: 'Héréd. Nat..' 1847, tom. i. p. 175.

[50] 'Hist. des Anomalies,' tom. iii. p. 499.

[51] Ibid., tom. iii. pp. 392, 502. The several memoirs by M. Dareste hereafter referred to are of special value on this whole subject.

[52] *See* his interesting work, 'Métamorphoses de l'Homme,' &c., 1862, p. 129.

In accordance with the facts above given, which prove that in many cases a close relation exists between variability and the sterility following from changed conditions, we may conclude that the exciting cause often acts at the earliest possible period, namely, on the sexual elements, before impregnation has taken place. That an affection of the female sexual element may induce variability we may likewise infer as probable from the occurrence of bud-variations; for a bud seems to be the analogue of an ovule. But the male element is apparently much oftener affected by changed conditions, at least in a visible manner, than the female element or ovule; and we know from Gärtner's and Wichura's statements that a hybrid used as the father and crossed with a pure species gives a greater degree of variability to the offspring, than does the same hybrid when used as the mother. Lastly, it is certain that variability may be transmitted through either sexual element, whether or not originally excited in them, for Kölreuter and Gärtner [53] found that when two species were crossed, if either one was variable, the offspring were rendered variable.

Summary.—From the facts given in this chapter, we may conclude that the variability of organic beings under domestication, although so general, is not an inevitable contingent on life, but results from the conditions to which the parents have been exposed. Changes of any kind in the conditions of life, even extremely slight changes, often suffice to cause variability. Excess of nutriment is perhaps the most efficient single exciting cause. Animals and plants continue to be variable for an immense period after their first domestication; but the conditions to which they are exposed never long remain quite constant. In the course of time they can be habituated to certain changes, so as to become less variable; and it is possible that when first domesticated they may have been even more variable than at present. There is good evidence that the power of changed conditions accumulates; so that two, three, or more generations must be exposed to new conditions before any effect is visible. The crossing of distinct forms, which have already become variable, increases in the offspring the tendency to further variability, by the unequal commingling of the characters of the two parents, by the reappearance of long-lost characters, and by the appearance of absolutely new characters. Some variations are induced by the direct action of the surrounding conditions on

[53] 'Dritte Fortsetzung,' &c., s. 123; 'Bastarderzeugung,' s. 249.

the whole organisation, or on certain parts alone; other variations appear to be induced indirectly through the reproductive system being affected, as we know is often the case with various beings, which when removed from their natural conditions become sterile. The causes which induce variability act on the mature organism, on the embryo, and, probably, on the sexual elements before impregnation has been effected.