CHAPTER XI.

ON BUD-VARIATION, AND ON CERTAIN ANOMALOUS MODES OF REPRODUCTION AND VARIATION.

BUD-VARIATION IN THE PEACH, PLUM, CHERRY, VINE, GOOSEBERRY, CURRANT, AND BANANA, AS SHOWN BY THE MODIFIED FRUIT—IN FLOWERS: CAMELLIAS, AZALEAS, CHRYSANTHEMUMS, ROSES, ETC.—ON THE RUNNING OF THE COLOUR IN CARNATIONS—BUD-VARIATIONS IN LEAVES—VARIATIONS BY SUCKERS, TUBERS, AND BULBS—ON THE BREAKING OF TULIPS—BUD-VARIATIONS GRADUATE INTO CHANGES CONSEQUENT ON CHANGED CONDITIONS OF LIFE—GRAFT-HYBRIDS—ON THE SEGREGATION OF THE PARENTAL CHARACTERS IN SEMINAL HYBRIDS BY BUD-VARIATION—ON THE DIRECT OR IMMEDIATE ACTION OF FOREIGN POLLEN ON THE MOTHER-PLANT—ON THE EFFECTS IN FEMALE ANIMALS OF A PREVIOUS IMPREGNATION ON THE SUBSEQUENT OFFSPRING—CONCLUSION AND SUMMARY.

THIS chapter will be chiefly devoted to a subject in many respects important, namely, bud-variation. By this term I include all those sudden changes in structure or appearance which occasionally occur in full-grown plants in their flower-buds or leaf-buds. Gardeners call such changes "Sports;" but this, as previously remarked, is an ill-defined expression, as it has often been applied to strongly marked variations in seedling plants. The difference between seminal and bud reproduction is not so great as it at first appears; for each bud is in one sense a new and distinct individual; but such individuals are produced through the formation of various kinds of buds without the aid of any special apparatus, whilst fertile seeds are produced by the concourse of the two sexual elements. The modifications which arise through bud-variation can generally be propagated to any extent by grafting, budding, cuttings, bulbs, &c., and occasionally even by seed. Some few of our most beautiful and useful productions have arisen by bud-variation.

Bud-variations have as yet been observed only in the vegetable kingdom; but it is probable that if compound animals, such as corals, &c., had been subjected to a long

course of domestication, they would have varied by buds; for they resemble plants in many respects. For instance, any new or peculiar character presented by a compound animal is propagated by budding, as occurs with differently coloured Hydras, and as Mr. Gosse has shown to be the case with a singular variety of a true coral. Varieties of the Hydra have also been grafted on other varieties, and have retained their character.

I will in the first place give all the cases of bud variations which I have been able to collect, and afterwards show their importance.[1] These cases prove that those authors who, like Pallas, attribute all variability to the crossing either of distinct races, or of distinct individuals belonging to the same race but somewhat different from each other, are in error; as are those authors who attribute all variability to the mere act of sexual union. Nor can we account in all cases for the appearance through bud-variation of new characters by the principle of reversion to long-lost characters. He who wishes to judge how far the conditions of life directly cause each particular variation ought to reflect well on the cases immediately to be given. I will commence with bud-variations, as exhibited in the fruit, and then pass on to flowers, and finally to leaves.

Peach (*Amygdalus persica*).—In the last chapter I gave two cases of a peach-almond and a double-flowered almond which suddenly produced fruit closely resembling true peaches. I have also given many cases of peach-trees producing buds, which, when developed into branches, have yielded nectarines. We have seen that no less than six named and several unnamed varieties of the peach have thus produced several varieties of nectarine. I have shown that it is highly improbable that all these peach-trees, some of which are old varieties, and have been propagated by the million, are hybrids from the peach and nectarine, and that it is opposed to all analogy to attribute the occasional production of nectarines

[1] Since the publication of the first edition of this work, I have found that M. Carrière, *Chef des Pépinières au Mus. d'Hist. Nat.*, in his excellent Essay, 'Production et Fixation des Variétés, 1865,' has given a list of bud-variations far more extensive than mine; but as these relate chiefly to cases occurring in France I have left my list as it stood, adding a few facts from M. Carrière and others. Any one who wishes to study the subject fully should refer to M. Carrière's Essay.

on peach-trees to the direct action of pollen from some neighbouring nectarine-tree. Several of the cases are highly remarkable, because, firstly, the fruit thus produced has sometimes been in part a nectarine and in part a peach; secondly, because nectarines thus suddenly produced have reproduced themselves by seed; and thirdly, because nectarines are produced from peach-trees from seed as well as from buds. The seed of the nectarine, on the other hand, occasionally produces peaches; and we have seen in one instance that a nectarine-tree yielded peaches by bud-variation. As the peach is certainly the oldest or primary variety, the production of peaches from nectarines, either by seeds or buds, may perhaps be considered as a case of reversion. Certain trees have also been described as indifferently bearing peaches or nectarines, and this may be considered as bud-variation carried to an extreme degree.

The *grosse mignonne* peach at Montreuil produced "from a sporting branch" the *grosse mignonne tardive*, "a most excellent variety," which ripens its fruit a fortnight later than the parent tree, and is equally good.[2] This same peach has likewise produced by bud-variation the *early grosse mignonne*. Hunt's large tawny nectarine "originated from Hunt's small tawny nectarine, but not through seminal reproduction."[3]

Plums.—Mr. Knight states that a tree of the yellow magnum bonum plum, forty years old, which had always borne ordinary fruit, produced a branch which yielded red magnum bonums.[4] Mr. Rivers, of Sawbridgeworth, informs me (Jan. 1863) that a single tree out of 400 or 500 trees of the Early Prolific plum, which is a purple kind, descended from an old French variety bearing purple fruit, produced when about ten years old bright yellow plums; these differed in no respect except colour from those on the other trees, but were unlike any other known kind of yellow plum.[5]

Cherry (*Prunus cerasus*).—Mr. Knight has recorded (ibid.) the case of a branch of a May-Duke cherry, which, though certainly never grafted, always produced fruit, ripening later, and more oblong than the fruit on the other branches. Another account has been given of two May-Duke cherry-trees in Scotland, with branches bearing oblong and very fine fruit, which invariably ripened, as in Knight's case, a fortnight later than the other cherries.[6] M. Carrière gives (p. 37) numerous analogous cases, and one of the same tree bearing three kinds of fruit.

Grapes (*Vitis vinifera*).—The black or purple Frontignan in

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[2] 'Gardener's Chron.,' 1854, p. 821.

[3] Lindley's 'Guide to Orchard,' as quoted in 'Gardener's Chron.' 1852, p. 821. For the *Early mignonne peach*, *see* 'Gardener's Chron.,' 1864, p. 1251.

[4] 'Transact. Hort. Soc.,' vol. ii. p. 160.

[5] *See* also 'Gardener's Chron., 1863, p. 27.

[6] 'Gard. Chron.,' 1852, p. 821.

one case produced during two successive years (and no doubt permanently) spurs which bore white Frontignan grapes. In another case, on the same footstalk, the lower berries "were well-coloured black Frontignans; those next the stalk were white, with the exception of one black and one streaked berry;" and altogether there were fifteen black and twelve white berries on the same stalk. In another kind of grape, black and amber-coloured berries were produced in the same cluster.[7] Count Odart describes a variety which often bears on the same stalk small round and large oblong berries; though the shape of the berry is generally a fixed character.[8] Here is another striking case given on the excellent authority of M. Carrière:[9] "a black Hamburg grape (Frankenthal) was cut down, and produced three suckers; one of these was layered, and after a time produced much smaller berries, which always ripened at least a fortnight earlier than the others. Of the remaining two suckers, one produced every year fine grapes, whilst the other, although it set an abundance of fruit, matured only a few, and these of inferior quality."

Gooseberry (*Ribes grossularia*).—A remarkable case has been described by Dr. Lindley[10] of a bush which bore at the same time no less than four kinds of berries, namely, hairy and red,—smooth, small and red,—green,—and yellow tinged with buff; the two latter kinds had a different flavour from the red berries, and their seeds were coloured red. Three twigs on this bush grew close together; the first bore three yellow berries and one red; the second twig bore four yellow and one red; and the third four red and one yellow. Mr. Laxton also informs me that he has seen a Red Warrington gooseberry bearing both red and yellow fruit on the same branch.

Currant (*Ribes rubrum*).—A bush purchased as the Champagne, which is a variety that bears blush-coloured fruit intermediate between red and white, produced during fourteen years on separate branches and mingled on the same branch, berries of the red, white, and champagne kinds.[11] The suspicion naturally arises that this variety may have originated from a cross between a red and white variety, and that the above transformation may be accounted for by reversion to both parent-forms; but from the foregoing complex case of the gooseberry this view is doubtful. In France, a branch of a red-currant bush, about ten years old, produced near the summit five white berries, and lower down, amongst the red berries,

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[7] Gardener's Chron.,' 1852, p. 629; 1856, p. 648; 1864, p. 986. Other cases are given by Braun, 'Rejuvenescence,' in 'Ray Soc. Bot. Mem.,' 1853, p. 314.

[8] 'Ampélographie,'&c., 1849, p. 71.

[9] 'Gardener's Chronicle,' 1866, p. 970.

[10] 'Gardener's Chronicle,' 1855, pp. 597, 612.

[11] 'Gardener's Chron.,' 1842, p. 873; 1855, p. 646. In the 'Chronicle,' p. 876, Mr. P. Mackenzie states that the bush still continues to bear the three kinds of fruit, "although they have not been every year alike.

one berry half red and half white.[12] Alexander Braun[13] also has often seen branches on white currant-trees bearing red berries.

Pear (*Pyrus communis*).—Dureau de la Malle states that the flowers on some trees of an ancient variety, the *doyenné galeux*, were destroyed by frost: other flowers appeared in July, which produced six pears; these exactly resembled in their skin and taste the fruit of a distinct variety, the *gros doyenne blanc*, but in shape were like the *bon-chrétien:* it was not ascertained whether this new variety could be propagated by budding or grafting. The same author grafted a *bon-chrétien* on a quince, and it produced, besides its proper fruit, an apparently new variety, of a peculiar form with thick and rough skin.[14]

Apple (*Pyrus malus*).—In Canada, a tree of the variety called Pound Sweet, produced,[15] between two of its proper fruit, an apple which was well russeted, small in size, different in shape, and with a short peduncle. As no russet apple grew anywhere near, this case apparently cannot be accounted for by the direct action of foreign pollen. M. Carrière (p. 38) mentions an analogous instance. I shall hereafter give cases of apple-trees which regularly produce fruit of two kinds, or half-and-half fruit; these trees are generally supposed, and probably with truth, to be of crossed parentage, and that the fruit reverts to both parent-forms.

Banana (*Musa sapientium*).—Sir R. Schomburgk states that he saw in St. Domingo a raceme on the Fig Banana which bore towards the base 125 fruits of the proper kind; and these were succeeded, as is usual, higher up the raceme, by barren flowers, and these by 420 fruits, having a widely different appearance, and ripening earlier than the proper fruit. The abnormal fruit closely resembled, except in being smaller, that of the *Musa chinensis* or *cavendishii*, which has generally been ranked as a distinct species.[16]

FLOWERS.—Many cases have been recorded of a whole plant, or single branch, or bud, suddenly producing flowers different from the proper type in colour, form, size, doubleness, or other character. Half the flower, or a smaller segment, sometimes changes colour.

Camellia.—The myrtle-leaved species (*C. myrtifolia*), and two or three varieties of the common species, have been known to produce hexagonal and imperfectly quadrangular flowers; and the branches producing such flowers have been propagated by grafting.[17] The Pompon variety often bears "four distinguishable kinds of flowers, "—the pure white and the red-eyed, which appear promiscuously; "the brindled pink and the rose-coloured, which may be kept

[12] 'Revue Horticole,' quoted in 'Gard. Chronicle,' 1844, p. 87.

[13] 'Rejuvenescence in Nature,' Bot. Memoirs Ray Soc.,' 1853, p. 314.

[14] 'Comptes Rendus,' tom. xli. 1855, p. 804. The second case is given on the authority of Gaudichaud, ibid., tom. xxxiv., 1852, p. 748.

[15] This case is given in the 'Gard. Chronicle,' 1867, p. 403.

[16] 'Journal of Proc. Linn. Soc., vol. ii. Botany, p. 131.

[17] 'Gard. Chronicle,' 1847, p. 207.

"separate with tolerable certainty by grafting from the branches "that bear them." A branch, also, on an old tree of the rose-coloured variety has been seen to "revert to the pure white colour, an "occurrence less common than the departure from it."[18]

Cratægus oxyacantha.—A dark pink hawthorn has been known to throw out a single tuft of pure white blossoms;[19] and Mr. A. Clapham, nurseryman, of Bedford, informs me that his father had a deep crimson thorn grafted on a white thorn, which during several years, always bore, high above the graft, bunches of white, pink and deep crimson flowers.

Azalea indica is well known often to produce new varieties by buds. I have myself seen several cases. A plant of *Azalea indica variegata* has been exhibited bearing a truss of flowers of *A. ind. gledstanesii* "as true as could possibly be produced, thus evidencing the origin of that fine variety." On another plant of *A. ind. variegata* a perfect flower of *A. ind. lateritia* was produced; so that both *gledstanesii* and *lateritia* no doubt originally appeared as sporting branches of *A. ind. variegata.*[20]

Hibiscus (*Paritium tricuspis*).—A seedling of this plant, when some years old, produced, at Saharunpore,[21] some branches "which bore leaves and flowers widely different from the normal form." "The abnormal leaf is much less divided, and not acuminated. The petals are considerably larger, and quite entire. There is also in the fresh state a conspicuous, large, oblong gland, full of a viscid secretion, on the back of each of the calycine segments." Dr. King, who subsequently had charge of these Gardens, informs me that a tree of *Paritium tricuspis* (probably the very same plant) growing there, had a branch buried in the ground, apparently by accident; and this branch changed its character wonderfully, growing like a bush, and producing flowers and leaves, resembling in shape those of another species, viz., *P. tiliaceum.* A small branch springing from this bush near the ground, reverted to the parent-form. Both forms were extensively propagated during several years by cuttings and kept perfectly true.

Althœa rosea.—A double yellow Hollyhock suddenly turned one year into a pure white single kind; subsequently a branch bearing the original double yellow flowers reappeared in the midst of the branches of the single white kind.[22]

Pelargonium.—These highly cultivated plants seem eminently liable to bud-variation. I will give only a few well-marked cases. Gärtner has seen[23] a plant of *P. zonale* with a branch having white

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[18] Herbert, 'Amaryllidaceæ,' 1838, p. 369.

[19] 'Gardener's Chronicle,' 1843, p. 391.

[20] Exhibited at Hort. Soc., London. Report in 'Gardener's Chron.,' 1844, p. 337.

[21] Mr. W. Bell, Bot. Soc. of Edinburgh, May, 1863.

[22] 'Revue Horticole,' quoted in 'Gardener's Chron.,' 1845, p. 475.

[23] 'Bastarderzeugung, 1849, s. 76.

edges, which remained constant for years, and bore flowers of a deeper red than usual. Generally speaking, such branches present little or no difference in their flowers: thus a writer[24] pinched off the leading shoot of a seedling *P. zonale*, and it threw out three branches, which differed in the size and colour of their leaves and stems; but on all three branches "the flowers were identical," except in being largest in the green-stemmed variety, and smallest in that with variegated foliage: these three varieties were subsequently propagated and distributed. Many branches, and some whole plants, of a variety called *compactum*, which bears orange-scarlet flowers, have been seen to produce pink flowers.[25] Hill's Hector, which is a pale red variety, produced a branch with lilac flowers, and some trusses with both red and lilac flowers. This apparently is a case of reversion, for Hill's Hector was a seedling from a lilac variety.[26] Here is a better case of reversion: a variety produced from a complicated cross, after having been propagated for five generations by seed, yielded by bud-variation three very distinct varieties which were undistinguishable from plants, "known to have been at some time ancestors of the plant in question."[27] Of all Pelargoniums, Rollisson's Unique seems to be the most sportive; its origin is not positively known, but is believed to be from a cross. Mr. Salter, of Hammersmith, states[28] that he has himself known this purple variety to produce the lilac, the rose-crimson or *conspicuum*, and the red or *coccineum* varieties; the latter has also produced the *rose d'amour*; so that altogether four varieties have originated by bud variation from Rollisson's Unique. Mr. Salter remarks that these four varieties "may now be con-" sidered as fixed, although they occasionally produce flowers of " the original colour. This year *coccineum* has pushed flowers of " three different colours, red, rose, and lilac, upon the same truss, " and upon other trusses are flowers half red and half lilac." Besides these four varieties, two other scarlet Uniques are known to exist, both of which occasionally produce lilac flowers identical with Rollisson's Unique;[29] but one at least of these did not arise through bud-variation, but is believed to be a seedling from Rollisson's Unique."[30] There are, also, in the trade[31] two other slightly different varieties, of unknown origin, of Rollisson's Unique: so that altogether we have a curiously complex case of variation both by buds and seeds.[32] Here is a still more complex case: M. Rafarin

[24] 'Journal of Horticulture,' 1861, p. 336.

[25] W. P. Ayres, in 'Gardener's Chron.,' 1842, p. 791.

[26] W. P. Ayres, ibid.

[27] Dr. Maxwell Masters, 'Pop. Science Review,' July, 1872, p. 250.

[28] 'Gardener's Chron.,' 1861, p. 968.

[29] Ibid., 1861, p. 945.

[30] W. Paul, in 'Gardener's Chron.,' 1861, p. 968.

[31] Ibid., p. 945.

[32] For other cases of bud-variation in this same variety, *see* 'Gardener's Chron.,' 1861, pp. 578, 600, 925. For other distinct' cases of bud-variation in the genus Pelargonium, *see* 'Cottage Gardener,' 1860, p. 194.

states that a pale rose-coloured variety produced a branch bearing deep red flowers. "Cuttings were taken from this 'sport,' from "which 20 plants were raised, which flowered in 1867, when it was "found that scarcely two were alike." Some resembled the parent-form, some resembled the sport, some bore both kinds of flowers; and even some of the petals on the same flower were rose-coloured and others red.[33] An English wild plant, the *Geranium pratense*, when cultivated in a garden, has been seen to produce on the same plant both blue and white, and striped blue and white flowers.[34]

Chrysanthemum.—This plant frequently sports, both by its lateral branches and occasionally by suckers. A seedling raised by Mr. Salter has produced by bud-variation six distinct sorts, five different in colour and one in foliage, all of which are now fixed.[35] A variety called *cedo nulli* bears small yellow flowers, but habitually produces branches with white flowers; and a specimen was exhibited, which Prof. T. Dyer saw, before the Horticultural Society. The varieties which were first introduced from China were so excessively variable, "that it was extremely difficult to tell which was the original colour of the variety, and which was the sport." The same plant would produce one year only buff-coloured, and next year only rose-coloured flowers; and then would change again, or produce at the same time flowers of both colours. These fluctuating varieties are now all lost, and, when a branch sports into a new variety, it can generally be propagated and kept true; but, as Mr. Salter remarks, "every sport should be thoroughly tested in "different soils before it can be really considered as fixed, as many "have been known to run back when planted in rich compost; but "when sufficient care and time are expended in proving, there will "exist little danger of subsequent disappointment." Mr. Salter informs me that with all the varieties the commonest kind of bud-variation is the production of yellow flowers, and, as this is the primordial colour, these cases may be attributed to reversion. Mr. Salter has given me a list of seven differently coloured chrysanthemums, which have all produced branches with yellow flowers; but three of them have also sported into other colours. With any change of colour in the flower, the foliage generally changes in a corresponding manner in lightness or darkness.

Another Compositous plant, namely, *Centauria cyanus*, when cultivated in a garden, not unfrequently produces on the same root flowers of four different colours, viz., blue, white, dark-purple, and parti-coloured.[36] The flowers of Anthemis also vary on the same plant.[37]

Roses.—Many varieties of the Rose are known or are believed to

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[33] Dr. Maxwell Masters, 'Pop. Science Review,' July, 1872, p. 254.

[34] Rev. W. T. Bree, in Loudon's 'Gard. Mag.,' vol. viii., 1832, p. 93.

[35] 'The Chrysanthemum: its History and Culture,' by J. Salter, 1865, p. 41, &c.

[36] Bree, in Loudon's 'Gard. Mag.,' vol. viii., 1832, p. 93.

[37] Bronn, 'Geschichte der Natur,' B. ii. s. 123.

have originated by bud-variation.[38] The common double moss-rose was imported into England from Italy about the year 1735.[39] Its origin is unknown, but from analogy it probably arose from the Provence rose (*R. centifolia*) by bud-variation; for the branches of the common moss-rose have several times been known to produce Provence roses, wholly or partially destitute of moss: I have seen one such instance, and several others have been recorded.[40] Mr. Rivers also informs me that he raised two or three roses of the Provence class from seed of the old single moss-rose;[41] and this latter kind was produced in 1807 by bud-variation from the common moss-rose. The white moss-rose was also produced in 1788 by an offset from the common red moss-rose: it was at first pale blush-coloured, but became white by continued budding. On cutting down the shoots which had produced this white moss-rose, two weak shoots were thrown up, and buds from these yielded the beautiful striped moss-rose. The common moss-rose has yielded by bud-variation, besides the old single red moss-rose, the old scarlet semi-double moss-rose, and the sage-leaf moss-rose, which "has a delicate shell-like form, and is of a beautiful blush colour; it is now (1852) nearly extinct."[42] A white moss-rose has been seen to bear a flower half white and half pink.[43] Although several moss-roses have thus certainly arisen by bud-variation, the greater number probably owe their origin to seed of moss-roses. For Mr. Rivers informs me that his seedlings from the old single moss-rose almost always produced moss-roses; and the old single moss-rose was, as we have seen, the product by bud-variation of the double moss-rose originally imported from Italy. That the original moss-rose was the product of bud-variation is probable, from the facts above given and from the de Meaux moss-rose (also a variety of *R. centifolia*)[44] having appeared as a sporting branch on the common rose de Meaux. Prof. Caspary has carefully described[45] the case of a six-year-old white moss-rose, which sent up several suckers, one of which was thorny, and produced red flowers, destitute of moss, exactly like those of the Provence rose (*R. centifolia*): another shoot bore both kinds of flowers, and in addition longitudinally striped flowers. As this white moss-rose had been grafted on the Provence rose, Prof. Caspary attributes the above

[38] T. Rivers, 'Rose Amateur's Guide,' 1837, p. 4.

[39] Mr. Shailer, quoted in 'Gardener's Chron.,' 1848, p. 759.

[40] 'Transact. Hort. Soc.,' vol. iv. 1822, p. 137; 'Gard. Chron.,' 1842, p. 422.

[41] *See* also Loudon's 'Arboretum,' vol. ii. p. 780.

[42] All these statements on the origin of the several varieties of the moss-rose are given on the authority of Mr. Shailer, who, together with his father, was concerned in their original propagation. *See* 'Gard. Chron.,' 1852, p. 759.

[43] 'Gard. Chron.,' 1845, p. 564.

[44] 'Transact. Hort. Soc.,' vol. ii. p. 242.

[45] 'Schriften der Phys. Oekon. Gesell. zu Königsberg,' Feb. 3, 1865, s. 4. *See* also Dr. Caspary's paper in 'Transactions of the Hort. Congress of Amsterdam,' 1865.

changes to the influence of the stock; but from the facts already given, and from others to be given, bud-variation, with reversion, is probably a sufficient explanation.

Many other instances could be added of roses varying by buds. The white Provence rose apparently originated in this way.[46] M. Carrière states (p. 36) that he himself knows of five varieties thus produced by the Baronne Prévost. The double and highly-coloured Belladonna rose has produced by suckers both semi-double and almost single white roses;[47] whilst suckers from one of these semi-double white roses reverted to perfectly characterised Belladonnas. In St. Domingo, varieties of the China rose propagated by cuttings often revert after a year or two into the old China rose.[48] Many cases have been recorded of roses suddenly becoming striped or changing their character by segments: some plants of the Comtesse de Chabrillant, which is properly rose-coloured, were exhibited in 1862,[49] with crimson flakes on a rose ground. I have seen the Beauty of Billiard with a quarter and with half the flower almost white. The Austrian bramble (*R. lutea*) not rarely[50] produces branches with pure yellow flowers; and Prof. Henslow has seen exactly half the flower of a pure yellow, and I have seen narrow yellow streaks on a single petal, of which the rest was of the usual copper colour.

The following cases are highly remarkable. Mr. Rivers, as I am informed by him, possessed a new French rose with delicate smooth shoots, pale glaucous-green leaves, and semi-double pale flesh-coloured flowers striped with dark red; and on branches thus characterised there suddenly appeared in more than one instance, the famous old rose called the Baronne Prévost, with its stout thorny shoots, and immense, uniformly and richly coloured double flowers; so that in this case the shoots, leaves, and flowers, all at once changed their character by bud-variation. According to M. Verlot,[51] a variety called *Rosa cannabifolia*, which has peculiarly shaped leaflets, and differs from every member of the family in the leaves being opposite instead of alternate, suddenly appeared on a plant of *R. alba* in the gardens of the Luxembourg. Lastly, "a running shoot" was observed by Mr. H. Curtis[52] on the old Aimée Vibert Noisette, and he budded it on Celine; thus a climbing Aimée Vibert was first produced and afterwards propagated.

Dianthus.—It is quite common with the Sweet William (*D. barbatus*) to see differently coloured flowers on the same root; and I have observed on the same truss four differently coloured and shaded flowers. Carnations and pinks (*D. caryophyllus*, &c.) occa-

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[46] 'Gard. Chron.,' 1852, p. 759.

[47] 'Transact. Hort. Soc.,' vol. ii. p. 242.

[48] Sir R. Schomburgk, 'Proc. Linn. Soc. Bot.,' vol. ii. p. 132.

[49] 'Gard. Chron.,' 1862, p. 619.

[50] Hopkirk's 'Flora Anomala,' 167.

[51] 'Sur la Production et la Fixation des Variétés,' 1865, p. 4.

[52] 'Journal of Horticulture,' March, 1865, p. 233.

sionally vary by layers; and some kinds are so little certain in character that they are called by floriculturists "catch-flowers."[53] Mr. Dickson has ably discussed the "running" of particoloured or striped carnations, and says it cannot be accounted for by the compost in which they are grown: "layers from the same clean "flower would come part of them clean and part foul, even when "subjected to precisely the same treatment; and frequently one "flower alone appears influenced by the taint, the remainder coming "perfectly clean."[54] This running of the parti-coloured flowers apparently is a case of reversion by buds to the original uniform tint of the species.

I will briefly mention some other cases of bud-variation to show how many plants belonging to many orders have varied in their flowers; and many others might be added. I have seen on a snap-dragon (*Antirrhinum majus*) white, pink, and striped flowers on the same plant, and branches with striped flowers on a red-coloured variety. On a double stock (*Mathiola incana*) I have seen a branch bearing single flowers; and on a dingy-purple double variety of the wall-flower (*Cheiranthus cheiri*), a branch which had reverted to the ordinary copper colour. On other branches of the same plant, some flowers were exactly divided across the middle, one half being purple and the other coppery; but some of the smaller petals towards the centre of these same flowers were purple longitudinally streaked with coppery colour, or coppery streaked with purple. A Cyclamen[55] has been observed to bear white and pink flowers of two forms, the one resembling the Persicum strain, and the other the Coum strain. *Oenothera biennis* has been seen[56] bearing flowers of three different colours. The hybrid *Gladiolus colvilii* occasionally bears uniformly coloured flowers, and one case is recorded[57] of all the flowers on a plant thus changing colour. A Fuchsia has been seen[58] bearing two kinds of flowers. *Mirabilis jalapa* is eminently sportive, sometimes bearing on the same root pure red, yellow, and white flowers, and others striped with various combinations of these three colours.[59] The plants of the Mirabilis, which bear such extraordinarily variable flowers in most, probably in all, cases, owe their origin, as shown by Prof. Lecoq, to crosses between differently coloured varieties.

Leaves and Shoots.—Changes, through bud-variation, in fruits and flowers have hitherto been treated of; incidentally some remarkable modifications in the leaves and shoots of the rose and Paritium, and

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[53] 'Gard. Chron.,' 1843, p. 135.

[54] Ibid., 1842, p. 55.

[55] 'Gard. Chron.,' 1867, p. 235.

[56] Gärtner, 'Bastarderzeugung,' s. 305.

[57] Mr. D. Beaton, in 'Cottage Gardener,' 1860, p. 250.

[58] 'Gard. Chron.,' 1850, p. 536.

[59] Braun, 'Ray Soc. Bot. Mem.' 1853, p. 315; Hopkirk's 'Flora Anomala,' p. 164; Lecoq, 'Géograph. Bot. de l'Europe,' tom. iii., 1854, p. 405; and 'De la Fécondation,' 1862, p. 303.

in a lesser degree in the foliage of the Pelargonium and Chrysanthemum, have been noticed. I will now add a few more cases of variation in leaf-buds. Verlot[60] states that on *Aralia trifoliata*, which properly has leaves with three leaflets, branches frequently appear bearing simple leaves of various forms; these can be propagated by buds or by grafting, and have given rise, as he states, to several nominal species.

With respect to trees, the history of but few of the many varieties with curious or ornamental foliage is known; but several probably have originated by bud-variation. Here is one case:—An old ash-tree (*Fraxinus excelsior*) in the grounds of Necton, as Mr. Mason states, "for many years has had one bough of a totally different character to the rest of the tree, or of any other ash-tree which I have seen; being short-jointed and densely covered with foliage." It was ascertained that this variety could be propagated by grafts.[61] The varieties of some trees with cut leaves, as the oak-leaved laburnum, the parsley-leaved vine, and especially the fern-leaved beech, are apt to revert by buds to the common forms.[62] The fern-like leaves of the beech sometimes revert only partially, and the branches display here and there sprouts bearing common leaves, fern-like, and variously shaped leaves. Such cases differ but little from the so-called heterophyllus varieties, in which the tree habitually bears leaves of various forms; but it is probable that most heterophyllous trees have originated as seedlings. There is a sub-variety of the weeping willow with leaves rolled up into a spiral coil; and Mr. Masters states that a tree of this kind kept true in his garden for twenty-five years, and then threw out a single upright shoot bearing flat leaves.[63]

I have often noticed single twigs and branches on beech and other trees with their leaves fully expanded before those on the other branches had opened; and as there was nothing in their exposure or character to account for this difference, I presume that they had appeared as bud-variations, like the early and late fruit-maturing varieties of the peach and nectarine.

Cryptogamic plants are liable to bud-variation, for fronds on the same fern often display remarkable deviations of structure. Spores, which are of the nature of buds, taken from such abnormal fronds, reproduce, with remarkable fidelity, the same variety, after passing through the sexual stage.[64]

With respect to colour, leaves often become by bud-variation zoned, blotched, or spotted with white, yellow, and red; and this

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[60] 'Des Variétés,' 1865, p. 5.

[61] W. Mason, in 'Gard. Chron.,' 1843, p. 878.

[62] Alex. Braun, 'Ray Soc. Bot. Mem.,' 1853, p. 315; 'Gard. Chron.,' 1841, p. 329.

[63] Dr. M. T. Masters, 'Royal Institution Lecture,' March 16, 1860.

[64] *See* Mr. W. K. Bridgman's curious paper in 'Annals and Mag. of Nat. Hist.,' December, 1861; also Mr. J. Scott, 'Bot. Soc. Edinburgh,' June 12, 1862.

occasionally occurs even with plants in a state of nature. Variegation, however, appears still more frequently in plants produced from seed; even the cotyledons or seed-leaves being thus affected.[65] There have been endless disputes whether variegation should be considered as a disease. In a future chapter we shall see that it is much influenced, both in the case of seedlings and of mature plants, by the nature of the soil. Plants which have become variegated as seedlings, generally transmit their character by seed to a large proportion of their progeny; and Mr. Salter has given me a list of eight genera in which this occurred.[66] Sir F. Pollock has given me more precise information: he sowed seed from a variegated plant of *Ballota nigra* which was found growing wild, and thirty per cent. of the seedlings were variegated; seed from these latter being sown, sixty per cent. came up variegated. When branches become variegated by bud-variation, and the variety is attempted to be propagated by seed, the seedlings are rarely variegated: Mr. Salter found this to be the case with plants belonging to eleven genera, in which the greater number of the seedlings proved to be green-leaved; yet a few were slightly variegated, or were quite white, but none were worth keeping. Variegated plants, whether originally produced from seeds or buds, can generally be propagated by budding, grafting, &c.; but all are apt to revert by bud-variation to their ordinary foliage. This tendency, however, differs much in the varieties of even the same species; for instance, the golden-striped variety of *Euonymus japonicus* "is very liable to run back to the green-leaved, while the silver-striped variety hardly ever changes."[67] I have seen a variety of the holly, with its leaves having a central yellow patch, which had everywhere partially reverted to the ordinary foliage, so that on the same small branch there were many twigs of both kinds. In the pelargonium, and in some other plants, variegation is generally accompanied by some degree of dwarfing, as is well exemplified in the "Dandy" pelargonium. When such dwarf varieties sport back by buds or suckers to the ordinary foliage, the dwarfed stature still remains.[68] It is remarkable that plants propagated from branches which have reverted from variegated to plain leaves[69] do not always (or never, as one observer asserts) perfectly resemble the original plain-leaved plant from which the variegated branch arose: it seems that a plant, in passing by bud-variation from plain leaves to variegated, and back again from variegated to plain, is generally in some degree affected so as to assume a slightly different aspect.

Bud-variation by Suckers, Tubers, and Bulbs.—All the cases hitherto given of bud-variation in fruits, flowers, leaves, and shoots, have been confined to buds on the stems or branches, with the

[65] 'Journal of Horticulture,' 1861, p. 336; Verlot, 'Des Variétés,' p. 76.

[66] *See* also Verlot, 'Des Variétés,' p. 74.

[67] 'Gard. Chron.,' 1844, p. 86.

[68] Ibid., 1861, p. 968.

[69] Ibid., 1861, p. 433; 'Cottage Gardener,' 1860, p. 2.

exception of a few cases incidentally noticed of varying suckers in the rose, pelargonium, and chrysanthemum. I will now give a few instances of variation in subterranean buds, that is, by suckers, tubers, and bulbs; not that there is any essential difference between buds above and beneath the ground. Mr. Salter informs me that two variegated varieties of Phlox originated as suckers; but I should not have thought these worth mentioning, had not Mr. Salter found, after repeated trials, that he could not propagate them by "root-joints," whereas, the variegated *Tussilago farfara* can thus be safely propagated;[70] but this latter plant may have originated as a variegated seedling, which would account for its greater fixedness of character. The Barberry (*Berberis vulgaris*) offers an analogous case; there is a well-known variety with seedless fruit, which can be propagated by cuttings or layers; but suckers always revert to the common form, which produces fruit containing seeds.[71] My father repeatedly tried this experiment, and always with the same result. I may here mention that maize and wheat sometimes produce new varieties from the stock or root, as does the sugar-cane.[72]

Turning now to tubers: in the common Potato (*Solanum tuberosum*) a single bud or eye sometimes varies and produces a new variety; or, occasionally, and this is a much more remarkable circumstance, all the eyes in a tuber vary in the same manner and at the same time, so that the whole tuber assumes a new character. For instance, a single eye in a tuber of the old *Forty-fold potato*, which is a purple variety, was observed[73] to become white; this eye was cut out and planted separately, and the kind has since been largely propagated. *Kemp's potato* is properly white, but a plant in Lancashire produced two tubers which were red, and two which were white; the red

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[70] M. Lemoine (quoted in 'Gard. Chron.,' 1867, p. 74) has lately observed that the Symphytum with variegated leaves cannot be propagated by division of the roots. He also found that out of 500 plants of a Phlox with striped flowers, which had been propagated by root-division, only seven or eight produced striped flowers. See also, on striped Pelargoniums, 'Gard. Chron.,' 1867, p. 1000.

[71] Anderson's 'Recreations in Agriculture,' vol. v. p. 152.

[72] For wheat, *see* 'Improvement of the Cereals,' by P. Shirreff, 1873, p. 47. For maize and sugar-cane, Carrière, ibid., pp. 40, 42. With respect to the sugar-cane, Mr. J. Caldwell, of Mauritius, says ('Gardener's Chronicle,' 1874, p. 316) the Ribbon cane has here "sported into a perfectly green cane and a perfectly red cane from the same head. I verified this myself, and saw at least 200 instances in the same plantation, and the fact has completely upset all our preconceived ideas of the difference of colour being permanent. The conversion of a striped cane into a green cane was not uncommon, but the change into a red cane universally disbelieved, and that both events should occur in the same plant incredible. I find, however, in Fleischman's 'Report on Sugar Cultivation in Louisiana for 1848, by the American Patent Office, the circumstance is mentioned, but he says he never saw it himself."

[73] 'Gard. Chron.,' 1857, p. 662.

kind was propagated in the usual manner by eyes, and kept true to its new colour, and, being found a more productive variety, soon became widely known under the name of *Taylor's Forty-fold*.[74] The old *Forty-fold potato*, as already stated, is a purple variety; but a plant long cultivated on the same ground produced, not, as in the case above given, a single white eye, but a whole white tuber, which has since been propagated and keeps true.[75] Several cases have been recorded of large portions of whole rows of potatoes slightly changing their character.[76]

Dahlias propagated by tubers under the hot climate of St. Domingo vary much; Sir R. Schomburgk gives the case of the "Butterfly variety," which the second year produced on the same plant "double and single flowers; here white petals edged with "maroon; there of a uniform deep maroon."[77] Mr. Bree also mentions a plant "which bore two different kinds of self-coloured "flowers, as well as a third kind which partook of both colours "beautifully intermixed."[78] Another case is described of a dahlia with purple flowers which bore a white flower streaked with purple.[79]

Considering how long and extensively many Bulbous plants have been cultivated, and how numerous are the varieties produced from seed, these plants have not perhaps varied so much by offsets, —that is, by the production of new bulbs,—as might have been expected. With the Hyacinth, however, several instances have been given by M. Carrière. A case also has been recorded of a blue variety which for three successive years gave offsets producing white flowers with a red centre.[80] Another hyacinth bore[81] on the same truss a perfectly pink and a perfectly blue flower. I have seen a bulb producing at the same time one stalk or truss with fine blue flowers, another with fine red flowers, and a third with blue flowers on one side and red on the other; several of the flowers being also longitudinally striped red and blue.

Mr. John Scott informs me that in 1862 *Imatophyllum miniatum*, in the Botanic Gardens of Edinburgh, threw up a sucker which differed from the normal form, in the leaves being two-ranked instead of four-ranked. The leaves were also smaller, with the upper surface raised instead of being channelled.

In the propagation of *Tulips*, seedlings are raised, called *selfs* or *breeders*, which, "consist of one plain colour on a white or yellow. "bottom. These, being cultivated on a dry and rather poor soil, "become broken or variegated and produce new varieties. The "time that elapses before they break varies from one to twenty

[74] 'Gard. Chron.,' 1841, p. 814.
[75] Ibid., 1857, p. 613.
[76] Ibid., 1857, p. 679. *See* also Philips, 'Hist. of Vegetables,' vol. ii. p. 91, for other and similar accounts.
[77] 'Journal of Proc. Linn. Soc.,' vol. ii. Botany, p. 132.
[78] Loudon's 'Gard. Mag.,' vol. viii., 1832, p. 94.
[79] 'Gard. Chron.,' 1850, p. 536; and 1842, p. 729.
[80] 'Des Jacinthes,' &c., Amsterdam, 1768, p. 122.
[81] 'Gard. Chron.,' 1845, p. 212.

" years or more, and sometimes this change never takes place."[82] The broken or variegated colours which give value to all tulips are due to bud-variation; for although the Bybloemens and some other kinds have been raised from several distinct breeders, yet all the Baguets are said to have come from a single breeder or seedling. This bud-variation, in accordance with the views of MM. Vilmorin and Verlot,[83] is probably an attempt to revert to that uniform colour which is natural to the species. A tulip, however, which has already become broken, when treated with too strong manure, is liable to flush or lose by a second act of reversion its variegated colours. Some kinds, as Imperatrix Florum, are much more liable than others to flushing; and Mr. Dickson maintains[84] that this can no more be accounted for than the variation of any other plant. He believes that English growers, from care in choosing seed from broken flowers instead of from plain flowers, have to a certain extent diminished the tendency in flowers already broken to flushing or secondary reversion. *Iris xiphium*, according to M. Carrière (p. 65), behaves in nearly the same manner, as do so many tulips.

During two consecutive years all the early flowers in a bed of *Tigridia conchiflora*[85] resembled those of the old *T. pavonia*; but the later flowers assumed their proper colour of fine yellow, spotted with crimson. An apparently authentic account has been published[86] of two forms of Hemerocallis, which have been universally considered as distinct species, changing into each other; for the roots of the large-flowered tawny *H. fulva*, being divided and planted in a different soil and place, produced the small-flowered *H. flava*, as well as some intermediate forms. It is doubtful whether such cases as these latter, as well as the "flushing" of broken tulips and the "running" of particoloured carnations,—that is, their more or less complete return to a uniform tint,—ought to be classed under bud-variation, or ought to be retained for the chapter in which I treat of the direct action of the conditions of life on organic beings. These cases, however, have this much in bud-variation, that the change is effected through buds and not through seminal reproduction. But, on the other hand, there is this difference—that in ordinary cases of bud-variation, one bud alone changes, whilst in the foregoing cases all the buds on the same plant were modified together. With the potato, we have seen an intermediate case, for all the eyes in one tuber simultaneously changed their character.

I will conclude with a few allied cases, which may be ranked either under bud-variation, or under the direct action of the conditions of life. When the common Hepatica is transplanted from

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[82] Loudon's 'Encyclopædia of Gardening,' p. 1024.

[83] 'Production des Variétés,' 1865, p. 63.

[84] 'Gard. Chron.,' 1841, p. 782; 1842, p. 55.

[85] 'Gard. Chron.,' 1849, p. 565.

[86] 'Transact. Linn. Soc.,' vol. ii. p. 354.

its native woods, the flowers change colour, even during the first year.[87] It is notorious that the improved varieties of the Heartsease (*Viola tricolor*), when transplanted, often produce flowers widely different in size, form, and colour: for instance, I transplanted a large uniformly-coloured dark purple variety, whilst in full flower, and it then produced much smaller, more elongated flowers, with the lower petals yellow; these were succeeded by flowers marked with large purple spots, and ultimately, towards the end of the same summer, by the original large dark purple flowers. The slight changes which some fruit-trees undergo from being grafted and regrafted on various stocks,[88] were considered by Andrew Knight[89] as closely allied to "sporting branches," or bud-variations. Again, we have the case of young fruit-trees changing their character as they grow old; seedling pears, for instance, lose with age their spines and improve in the flavour of their fruit. Weeping birch-trees, when grafted on the common variety, do not acquire a perfect pendulous habit until they grow old: on the other hand, I shall hereafter give the case of some weeping ashes which slowly and gradually assumed an upright habit of growth. All such changes, dependent on age, may be compared with the changes, alluded to in the last chapter, which many trees naturally undergo; as in the case of the Deodar and Cedar of Lebanon, which are unlike in youth, whilst they closely resemble each other in old age; and as with certain oaks, and with some varieties of the lime and hawthorn.[90]

Graft-hybrids.—Before giving a summary on Bud-variation I will discuss some singular and anomalous cases, which are more or less closely related to this same subject. I will begin with the famous case of Adam's laburnum or *Cytisus adami*, a form or hybrid intermediate between two very distinct species, namely, *C. laburnum* and *purpureus*, the common and purple laburnum; but as this tree has often been described, I will be as brief as I can.

Throughout Europe, in different soils and under different climates,

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[87] Godron, 'De l'Espèce,' tom. ii. p. 84.

[88] M. Carrière has lately described, in the 'Revue Horticole,' (Dec. 1, 1866, p. 457,) an extraordinary case. He twice inserted grafts of the *Aria vestita* on thorn-trees (*épines*) growing in pots; and the grafts, as they grew, produced shoots with bark, buds, leaves, petioles, petals, and flower-stalks, all widely different from those of the Aria. The grafted shoots were also much hardier, and flowered earlier, than those on the ungrafted Aria.

[89] 'Transact. Hort. Soc.,' vol ii. p. 160.

[90] For the cases of oaks, *see* Alph. De Candolle in 'Bibl. Univers.,' Geneva, Nov. 1862; for limes, &c., Loudon's 'Gard Mag.,' vol. xi., 1835, p. 503.

branches on this tree have repeatedly and suddenly reverted to the two parent-species in their flowers and leaves. To behold mingled on the same tree tufts of dingy-red, bright yellow, and purple flowers, borne on branches having widely different leaves and manner of growth, is a surprising sight. The same raceme sometimes bears two kinds of flowers; and I have seen a single flower exactly divided into halves, one side being bright yellow and the other purple; so that one half of the standard-petal was yellow and of larger size, and the other half purple and smaller. In another flower the whole corolla was bright yellow, but exactly half the calyx was purple. In another, one of the dingy-red wing-petals had a narrow bright yellow stripe on it; and lastly, in another flower, one of the stamens, which had become slightly foliaceous, was half yellow and half purple; so that the tendency to segregation of character or reversion affects even single parts and organs.[91] The most remarkable fact about this tree is that in its intermediate state, even when growing near both parent-species, it is quite sterile; but when the flowers become pure yellow or pure purple they yield seed. I believe that the pods from the yellow flowers yield a full complement of seed; they certainly yield a larger number. Two seedlings raised by Mr. Herbert from such seed[92] exhibited a purple tinge on the stalks of their flowers; but several seedlings raised by myself resembled in every character the common laburnum, with the exception that some of them had remarkably long racemes: these seedlings were perfectly fertile. That such purity of character and fertility should be suddenly reacquired from so hybridised and sterile a form is an astonishing phenomenon. The branches with purple flowers appear at first sight exactly to resemble those of *C. purpureus;* but on careful comparison I found that they differed from the pure species in the shoots being thicker, the leaves a little broader, and the flowers slightly shorter, with the corolla and calyx less brightly purple: the basal part of the standard-petal also plainly showed a trace of the yellow stain. So that the flowers, at least in this instance, had not perfectly recovered their true character; and in accordance with this, they were not perfectly fertile, for many of the pods contained no seed, some produced one, and very few contained as many as two seeds; whilst numerous pods on a tree of the pure *C. purpureus* in my garden contained three, four, and five fine seeds. The pollen, moreover, was very imperfect, a multitude of grains being small and shrivelled; and this is a singular fact; for, as we shall immediately see, the pollen-grains in the dingy-red and sterile flowers on the parent-tree, were, in external appearance, in a much

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[91] For analogous facts, *see* Braun, 'Rejuvenescence,' in 'Ray Soc. Bot. Mem.,' 1853, p. 320; and 'Gard. Chron.,' 1842, p. 397; also Braun, in 'Sitzungsberichte der Ges. naturforschender Freunde,' June, 1873, p. 63.

[92] 'Journal of Hort. Soc.,' vol. ii. 1847, p. 100.

better state, and included very few shrivelled grains. Although the pollen of the reverted purple flowers was in so poor a condition, the ovules were well formed, and the seeds, when mature, germinated freely with me. Mr. Herbert raised plants from seeds of the reverted purple flowers, and they differed a *very little* from the usual state of *C. purpureus*. Some which I raised in the same manner did not differ at all, either in the character of their flowers or of the whole bush, from the pure *C. purpureus*.

Prof. Caspary has examined the ovules of the dingy-red and sterile flowers in several plants of *C. adami* on the Continent,[93] and finds them generally monstrous. In three plants examined by me in England, the ovules were likewise monstrous, the nucleus varying much in shape, and projecting irregularly beyond the proper coats. The pollen grains, on the other hand, judging from their external appearance, were remarkably good, and readily protruded their tubes. By repeatedly counting, under the microscope, the proportional number of bad grains, Prof. Caspary ascertained that only 2·5 per cent. were bad, which is a less proportion than in the pollen of three pure species of Cytisus in their cultivated state, viz., *C. purpureus, laburnum,* and *alpinus*. Although the pollen of *C. adami* is thus in appearance good, it does not follow, according to M. Naudin's observation[94] on Mirabilis, that it would be functionally effective. The fact of the ovules of *C. adami* being monstrous, and the pollen apparently sound, is all the more remarkable, because it is opposed to what usually occurs not only with most hybrids,[95] but with two hybrids in the same genus, namely in *C. purpureo-elongatus*, and *C. alpino-laburnum*. In both these hybrids, the ovules, as observed by Prof. Caspary and myself, were well-formed, whilst many of the pollen-grains were ill-formed; in the latter hybrid 20·3 per cent., and in the former no less than 84·8 per cent. of the grains were ascertained by Prof. Caspary to be bad. This unusual condition of the male and female reproductive elements in *C. adami* has been used by Prof. Caspary as an argument against this plant being considered as an ordinary hybrid produced from seed; but we should remember that with hybrids the ovules have not been examined nearly so frequently as the pollen, and they may be much oftener imperfect than is generally supposed. Dr. E. Bornet, of Antibes, informs me (through Mr. J. Traherne Moggridge) that with hybrid Cisti the ovarium is frequently deformed, the ovules being in some cases quite absent, and in other cases incapable of fertilisation.

Several theories have been propounded to account for the origin of *C. adami*, and for the transformations which it undergoes. The

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[93] *See* 'Transact. of Hort. Congress of Amsterdam,' 1865; but I owe most of the following information to Prof. Caspary's letters.

[94] 'Nouvelles Archives du Muséum,' tom. i. p. 143.

[95] *See* on this head, Naudin, ibid., p. 141.

whole case has been attributed by some authors to bud-variation; but considering the wide difference between *C. laburnum* and *purpureus*, both of which are natural species, and considering the sterility of the intermediate form, this view may be summarily rejected. We shall presently see that, with hybrid plants, two embryos differing in their characters may be developed within the same seed and cohere; and it has been supposed that *C. adami* thus originated. Many botanists maintain that *C. adami* is a hybrid produced in the common way by seed, and that it has reverted by buds to its two parent-forms. Negative results are not of much value; but Reisseck, Caspary, and myself, tried in vain to cross *C. laburnum* and *purpureus*; when I fertilised the former with pollen of the latter, I had the nearest approach to success, for pods were formed, but in sixteen days after the withering of the flowers, they fell off. Nevertheless, the belief that *C. adami* is a spontaneously produced hybrid between these two species is supported by the fact that such hybrids have arisen in this genus. In a bed of seedlings from *C. elongatus*, which grew near to *C. purpureus*, and was probably fertilised by it through the agency of insects (for these, as I know by experiment, play an important part in the fertilisation of the laburnum), the sterile hybrid *C. purpureo-elongatus* appeared.[96] Thus, also, Waterer's laburnum, the *C. alpino-laburnum*,[97] spontaneously appeared, as I am informed by Mr. Waterer, in a bed of seedlings.

On the other hand, we have a clear and distinct account given to Poiteau,[98] by M. Adam, who raised the plant, showing that *C. adami* is not an ordinary hybrid; but is what may be called a graft-hybrid, that is, one produced from the united cellular tissue of two distinct species. M. Adam inserted in the usual manner a shield of the bark of *C. purpureus* into a stock of *C. laburnum*; and the bud lay dormant, as often happens, for a year; the shield then produced many buds and shoots, one of which grew more upright and vigorous with larger leaves than the shoots of *C. purpureus*, and

[96] Braun, in 'Bot. Mem. Ray. Soc.,' 1853, p. xxiii.

[97] This hybrid has never been described. It is exactly intermediate in foliage, time of flowering, dark striæ at the base of the standard petal, hairiness of the ovarium, and in almost every other character, between *C. laburnum* and *alpinus*; but it approaches the former species more nearly in colour, and exceeds it in the length of the racemes. We have before seen that 20·3 per cent. of its pollen-grains are ill-formed and worthless. My plant, though growing not above thirty or forty yards from both parent-species, during some seasons yielded no good seeds; but in 1866 it was unusually fertile, and its long racemes produced from one to occasionally even four pods. Many of the pods contained no good seeds, but generally they contained a single apparently good seed, sometimes two, and in one case three seeds. Some of these seeds germinated, and I raised two trees from them; one resembles the present form; the other has a remarkable dwarf character with small leaves, but has not yet flowered.

[98] 'Annales de la Soc. de l'Hort. de Paris,' tom. vii., 1830, p. 93.

was consequently propagated. Now it deserves especial notice that these plants were sold by M. Adam, as a variety of *C. purpureus*, before they had flowered; and the account was published by Poiteau after the plants had flowered, but before they had exhibited their remarkable tendency to revert into the two parent species. So that there was no conceivable motive for falsification, and it is difficult to see how there could have been any error.[99] If we admit as true M. Adam's account, we must admit the extraordinary fact that two distinct species can unite by their cellular tissue, and subsequently produce a plant bearing leaves and sterile flowers intermediate in character between the scion and stock, and producing buds liable to reversion; in short, resembling in every important respect a hybrid formed in the ordinary way by seminal reproduction.

I will therefore give all the facts which I have been able to collect on the formation of hybrids between distinct species or varieties, without the intervention of the sexual organs. For if, as I am now convinced, this is possible, it is a most important fact, which will sooner or later change the views held by physiologists with respect to sexual reproduction. A sufficient body of facts will afterwards be adduced, showing that the segregation or separation of the characters of the two parent-forms by bud-variation, as in the case of *Cytisus adami*, is not an unusual though a striking phenomenon. We shall further see that a whole bud may thus revert, or only half, or some smaller segment.

The famous *bizzarria Orange* offers a strictly parallel case to that of *Cytisus adami*. The gardener who in 1644 in Florence raised this tree, declared that it was a seedling which had been grafted; and after the graft had perished, the stock sprouted and produced the bizzarria. Gallesio, who carefully examined several living specimens and compared them with the description given by the original describer, P. Nato,[100] states that the tree produces at the same time leaves, flowers, and fruit identical with the bitter orange and with the citron of Florence, and likewise compound fruit, with the two kinds either blended together, both externally and internally,

[99] An account was given in the 'Gardener's Chronicle' (1857, pp. 382, 400) of a common laburnum on which grafts of *C. purpureus* had been inserted, and which gradually assumed the character of *C. adami*; but I have little doubt that *C. adami* had been sold to the purchaser, who was not a botanist, in the place of *C. purpureus*. I have ascertained that this occurred in another instance.

[100] Gallesio, 'Gli Agrumi dei Giard. Bot. Agrar. di. Firenze,' 1839, p. 11. In his 'Traité du Citrus,' 1811, p. 146, he speaks as if the compound fruit consisted in part of a lemon, but this apparently was a mistake.

or segregated in various ways. This tree can be propagated by cuttings, and retains its diversified character. The so-called trifacial orange of Alexandria and Smyrna[101] resembles in its general nature the bizzarria, and differs only in the orange being of the sweet kind; this and the citron are blended together in the same fruit, or are separately produced on the same tree; nothing is known of its origin. In regard to the bizzarria, many authors believe that it is a graft-hybrid; Gallesio, on the other hand, thinks that it is an ordinary hybrid, with the habit of partially reverting by buds to the two parent-forms; and we have seen that the species in this genus often cross spontaneously.

It is notorious that when the variegated Jessamine is budded on the common kind, the stock sometimes produces buds bearing variegated leaves: Mr. Rivers, as he informs me, has seen instances of this. The same thing occurs with the Oleander.[102] Mr. Rivers, on the authority of a trustworthy friend, states that some buds of a golden-variegated ash, which were inserted into common ashes, all died except one; but the ash-stocks were affected,[103] and produced, both above and below the points of insertion of the plates of bark bearing the dead buds, shoots which bore variegated leaves. Mr. J. Anderson Henry has communicated to me a nearly similar case: Mr. Brown, of Perth, observed many years ago, in a Highland glen, an ash-tree with yellow leaves; and buds taken from this tree were inserted into common ashes, which in consequence were affected, and produced the *Blotched Breadalbane Ash*. This variety has been propagated, and has preserved its character during the last fifty years. Weeping ashes, also, were budded on the affected stocks, and became similarly variegated. It has been repeatedly proved that several species of Abutilon, on which the variegated *A. thompsonii* has been grafted, become variegated.[104]

Many authors consider variegation as the result of disease; and the foregoing cases may be looked at as the direct result of the inoculation of a disease or some weakness. This has been almost proved to be the case by Morren in the excellent paper just referred to, who shows that even a leaf inserted by its footstalk into the bark of the stock is sufficient to communicate variegation to it, though the leaf soon perishes. Even fully formed leaves on the stock of Abutilon are sometimes affected by the graft and become variegated. Variegation is much influenced, as we shall hereafter see, by the nature of the soil in which the plants are grown; and it does not

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[101] 'Gard. Chron.,' 1855, p. 628. *See* also Prof. Caspary, in 'Transact. Hort. Congress of Amsterdam,' 1865.

[102] Gärtner ('Bastarderzeugung,' s. 611) gives many references on this subject.

[103] A nearly similar account was given by Brabley, in 1724, in his 'Treatise on Husbandry,' vol. i. p. 199.

[104] Morren, 'Bull. de l'Acad. R. des Sciences de Belgique,' 2de séries, tom. xxviii., 1869, p. 434. Also Magnus, 'Gesellschaft naturforschender Freunde, Berlin,' Feb. 21, 1871, p. 13; ibid., June 21, 1870, and Oct. 17, 1871. Also 'Bot. Zeitung,' Feb. 24, 1871.

seem improbable that whatever change in the sap or tissues certain soils induce, whether or not called a disease, might spread from the inserted piece of bark to the stock. But a change of this kind cannot be considered to be of the nature of a graft-hybrid.

There is a variety of the hazel with dark-purple leaves, like those of the copper-beech: no one has attributed this colour to disease, and it apparently is only an exaggeration of a tint which may often be seen on the leaves of the common hazel. When this variety is grafted on the common hazel,[105] it sometimes colours, as has been asserted, the leaves below the graft; although negative evidence is not of much value, I may add that Mr. Rivers, who has possessed hundreds of such grafted trees, has never seen an instance.

Gärtner[106] quotes two separate accounts of branches of dark and white-fruited vines which had been united in various ways, such as being split longitudinally, and then joined, &c.; and these branches produced distinct bunches of grapes of the two colours, and other bunches with berries, either striped, or of an intermediate and new tint. Even the leaves in one case were variegated. These facts are the more remarkable because Andrew Knight never succeeded in raising variegated grapes by fertilising white kinds by pollen of dark kinds; though, as we have seen, he obtained seedlings with variegated fruits and leaves, by fertilising a white variety by the already variegated dark Aleppo grape. Gärtner attributes the above-quoted cases merely to bud-variation; but it is a strange coincidence that the branches which had been grafted in a peculiar manner should alone thus have varied; and H. Adorne de Tscharner positively asserts that he produced the described result more than once, and could do so at will, by splitting and uniting the branches in the manner described by him.

I should not have quoted the following case had not the author of 'Des Jacinthes'[107] impressed me with the belief not only of his extensive knowledge, but of his truthfulness: he says that bulbs of blue and red hyacinths may be cut in two, and that they will grow together and throw up a united stem (and this I have myself seen) with flowers of the two colours on the opposite sides. But the remarkable point is, that flowers are sometimes produced with the two colours blended together, which makes the case closely analogous with that of the blended colours of the grapes on the united vine branches.

In the case of roses it is supposed that several graft-hybrids have been formed, but there is much doubt about these cases, owing to the frequency of ordinary bud-variations. The most trustworthy instance known to me is one, recorded by Mr. Poynter,[108] who assures me in a letter of the entire accuracy of the statement. *Rosa devoniensis* had been budded some years previously on a white

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[105] Loudon's 'Arboretum,' vol. iv. p. 2595.

[106] 'Bastarderzeugung,' s. 619.

[107] Amsterdam, 1768, p. 124.

[108] 'Gard. Chron.,' 1860, p. 672, with a woodcut.

Banksian rose; and from the much enlarged point of junction, whence the Devoniensis and Banksian still continued to grow, a third branch issued, which was neither pure Banksian nor pure Devoniensis, but partook of the character of both; the flowers resembled, but were superior in character to those of the variety called *Lamarque* (one of the Noisettes), while the shoots were similar in their manner of growth to those of the Banksian rose, with the exception that the longer and more robust shoots were furnished with prickles. This rose was exhibited before the Floral Committee of the Horticultural Society of London. Dr. Lindley examined it and concluded that it had certainly been produced by the mingling of *R. banksiæ* with some rose like *R. devoniensis*, "for while it was very greatly increased in vigour and in size of all the parts, the leaves were half-way between a Banksian and Tea-scented rose." It appears that rose-growers were previously aware that the Banksian rose sometimes affects other roses. As Mr. Poynter's new variety is intermediate in its fruit and foliage between the stock and scion, and as it arose from the point of junction between the two, it is very improbable that it owes its origin to mere bud-variation, independently of the mutual influence of the stock and scion.

Lastly, with respect to potatoes. Mr. R. Trail stated in 1867 before the Botanical Society of Edinburgh (and has since given me fuller information), that several years ago he cut about sixty blue and white potatoes into halves through the eyes or buds, and then carefully joined them, destroying at the same time the other eyes. Some of these united tubers produced white, and others blue tubers; some, however, produced tubers partly white and partly blue; and the tubers from about four or five were regularly mottled with the two colours. In these latter cases we may conclude that a stem had been formed by the union of the bisected buds, that is, by graft-hybridisation.

In the 'Botanische Zeitung' (May 16, 1868), Professor Hildebrand gives an account with a coloured figure, of his experiments on two varieties which were found during the same season to be constant in character, namely, a somewhat elongated rough-skinned red potato and a rounded smooth white one. He inserted buds reciprocally into both kinds, destroying the other buds. He thus raised two plants, and each of these produced a tuber intermediate in character between the two parent-forms. That from the red bud grafted into the white tuber, was at one end red and rough, as the whole tuber ought to have been if not affected; in the middle it was smooth with red stripes, and at the other end smooth and altogether white like that of the stock.

Mr. Taylor, who had received several accounts of potatoes having been grafted by wedge-shaped pieces of one variety inserted into another, though sceptical on the subject, made twenty-four experiments which he described in detail before the Horticultural Society.[109]

[109] *See* 'Gard. Chron.,' 1869, p. 220.

He thus raised many new varieties, some like the graft or like the stock; others having an intermediate character. Several persons witnessed the digging up of the tubers from these graft-hybrids; and one of them, Mr. Jameson, a large dealer in potatoes, writes thus, "They were such a mixed lot, as I have never before or since "seen. They were of all colours and shapes, some very ugly and "some very handsome." Another witness says "some were round, "some kidney, pink-eyed kidney, piebald, and mottled red and "purple, of all shapes and sizes." Some of these varieties have been found valuable, and have been extensively propagated. Mr. Jameson took away a large piebald potato which he cut into five sets and propagated; these yielded round, white, red, and piebald potatoes.

Mr. Fitzpatrick followed a different plan;[110] he grafted together not the tubers but the young stems of varieties producing black, white, and red potatoes. The tubers borne by three of these twin or united plants were coloured in an extraordinary manner; one was almost exactly half black and half white, so that some persons on seeing it thought that two potatoes had been divided and rejoined; other tubers were half red and half white, or curiously mottled with red and white, or with red and black, according to the colours of the graft and stock.

The testimony of Mr. Fenn is of much value, as he is "a well known potato-grower" who has raised many new varieties by crossing different kinds in the ordinary manner. He considers it "demonstrated" that new, intermediate varieties can be produced by grafting the tubers, though he doubts whether such will prove valuable.[111] He made many trials and laid the results, exhibiting specimens, before the Horticultural Society. Not only were the tubers affected, some being smooth and white at one end, and rough and red at the other, but the stems and leaves were modified in their manner of growth, colour and precocity. Some of these graft-hybrids after being propagated for three years still showed in their haulms their new character, different from that of the kind from which the eyes had been taken. Mr. Fenn gave twelve of the tubers of the third generation to Mr. Alex. Dean, who grew them, and was thus converted into a believer in graft-hybridisation, having previously been a complete sceptic. For comparison he planted the pure parent-forms alongside the twelve tubers; and found that many of the plants from the latter[112] were intermediate between the two parent-forms in precocity, in the tallness, uprightness, jointing, and robustness of the stems, and in the size and colour of the leaves.

Another experimentalist, Mr. Rintoul, grafted no less than fifty-nine tubers, which differed in shape (some being kidneys) in smoothness

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[110] 'Gard. Chron.,' 1869, p. 335.

[111] 'Gard. Chron.,' 1869, p. 1018, with remarks by Dr. Masters on the adhesion of the united wedges. *See* also ibid., 1870, pp. 1277, 1283.

[112] 'Gard. Chron.,' 1871, p. 837.

and colour,[113] and many of the plants thus raised "were intermediate "in the tubers as well as in the haulms." He describes the more striking cases.

In 1871 I received a letter from Mr. Merrick, of Boston, U.S.A., who states that, "Mr. Fearing Burr, a very careful experimenter and "author of a much valued book, 'The Garden Vegetables of "America,' has succeeded in producing distinctly mottled and "most curious potatoes—evidently graft-hybrids, by inserting eyes "from blue or red potatoes into the substance of white ones, after "removing the eyes of the latter. I have seen the potatoes, and "they are very curious."

We will now turn to the experiments made in Germany, since the publication of Prof. Hildebrand's paper. Herr Magnus relates[114] the results of numerous trials made by Herren Reuter and Lindemuth, both attached to the Royal Gardens of Berlin. They inserted the eyes of red potatoes into white ones, and *vice versâ*. Many different forms partaking of the characters of the inserted bud and of the stock were thus obtained; for instance, some of the tubers were white with red eyes.

Herr Magnus also exhibited in the following year before the same Society (Nov. 19, 1872), the produce of grafts between black, white, and red potatoes, made by Dr. Neubert. These were made by uniting not the tubers but the young stems, as was done by Mr. Fitzpatrick. The result was remarkable, inasmuch as all the tubers thus produced were intermediate in character, though in a variable degree. Those between the black and the white or the red were the most striking in appearance. Some from between the white and red had one half of one colour and the other half of the other colour.

At the next meeting of the society Herr Magnus communicated the results of Dr. Heimann's experiments in grafting together the tubers of red Saxon, blue, and elongated white potatoes. The eyes were removed by a cylindrical instrument, and inserted into corresponding holes in other varieties. The plants thus produced yielded a great number of tubers, which were intermediate between the two parent-forms in shape, and in the colour both of the flesh and skin.

Herr Reuter experimented,[115] by inserting wedges of the elongated White Mexican potato into a Black Kidney potato. Both sorts are known to be very constant, and differ much not only in form and colour, but in the eyes of the Black Kidney being deeply sunk, whereas those of the White Mexican are superficial and of a different shape. The tubers produced by these hybrids were intermediate in colour and form; and some which resembled in form the graft, *i.e.* the Mexican, had eyes deeply sunk and of the same shape as in the stock or Black Kidney.

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[113] 'Gard. Chron.,' 1870, p. 1506.

[114] 'Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin,' Oct. 17, 1871.

[115] Ibid., Nov. 17, 1874. *See* also excellent remarks by Herr Magnus.

Any one who will attentively consider the abstract now given, of the experiments made by many observers in several countries, will, I think, be convinced that by grafting two varieties of the potato together in various ways, hybridised plants can be produced. It should be observed that several of the experimentalists are scientific horticulturists, and some of them potato-growers on a large scale, who, though beforehand sceptical, have been fully convinced of the possibility, even of the ease, of making graft-hybrids. The only way of escaping from this conclusion is to attribute all the many recorded cases to simple bud-variation. Undoubtedly the potato, as we have seen in this chapter, does sometimes, though not often, vary by buds; but it should be especially noted that it is experienced potato-growers, whose business it is to look out for new varieties, who have expressed unbounded astonishment at the number of new forms produced by graft-hybridisation. It may be argued that it is merely the operation of grafting, and not the union of two kinds, which causes so extraordinary an amount of bud-variation; but this objection is at once answered by the fact that potatoes are habitually propagated by the tubers being cut into pieces, and the sole difference in the case of graft-hybrids is that either a half or a smaller segment or a cylinder is placed in close opposition with the tissue of another variety. Moreover, in two cases, the young stems were grafted together, and the plants thus united yielded the same results as when the tubers were united. It is an argument of the greatest weight that when varieties are produced by simple bud-variation, they frequently present quite new characters; whereas in all the numerous cases above given, as Herr Magnus likewise insists, the graft-hybrids are intermediate in character between the two forms employed. That such a result should follow if the one kind did not affect the other is incredible.

Characters of all kinds are affected by graft hybridisation, in whatever way the grafting may have been effected. The plants thus raised yield tubers which partake of the widely different colours, form, state of surface, position and shape of the eye of the parents; and according to two careful observers they are also intermediate in certain constitutional

peculiarities. But we should bear in mind that in all the varieties of the potato, the tubers differ much more than any other part.

The potato affords the best evidence of the possibility of the formation of graft-hybrids, but we must not overlook the account given of the origin of the famous *Cytisus adami* by M. Adam, who had no conceivable motive for deception, and the exactly parallel account of the origin of the Bizzarria orange, namely by graft-hybridisation. Nor must the cases be undervalued in which different varieties or species of vines, hyacinths and roses, have been grafted together, and have yielded intermediate forms. It is evident that graft-hybrids can be made much more easily with some plants, as the potato, than with others, for instance our common fruit trees; for these latter have been grafted by the million during many centuries, and though the graft is often slightly affected, it is very doubtful whether this may not be accounted for, merely by a more or less free supply of nutriment. Nevertheless, the cases above given seem to me to prove that under certain unknown conditions graft-hybridisation can be effected.

Herr Magnus asserts with much truth that graft-hybrids resemble in all respects seminal hybrids, including their great diversity of character. There is, however, a partial exception, inasmuch as the characters of the two parent forms are not often homogeneously blended together in graft-hybrids. They much more commonly appear in a segregated condition, —that is, in segments either at first, or subsequently through reversion. It would seem that the reproductive elements are not so completely blended by grafting as by sexual generation. But segregation of this kind occurs by no means rarely, as will be immediately shown, in seminal hybrids. Finally it must, I think, be admitted that we learn from the foregoing cases a highly important physiological fact, namely, that the elements that go to the production of a new being, are not necessarily formed by the male and female organs. They are present in the cellular tissue in such a state that they can unite without the aid of the sexual organs, and thus give rise to a new bud partaking of the characters of the two parent-forms.

On the segregation of the parental characters in seminal hybrids by bud-variation.—I will now give a sufficient number of cases to show that segregation of this kind, namely, by buds, may occur in ordinary hybrids raised from seed.

Hybrids were raised by Gärtner between *Tropæolum minus* and *majus*[116] which at first produced flowers intermediate in size, colour, and structure between their two parents; but later in the season some of these plants produced flowers in all respects like those of the mother-form, mingled with flowers still retaining the usual intermediate condition. A hybrid Cereus between *C. speciosissimus* and *phyllanthus*,[117] plants which are widely different in appearance, produced for the first three years angular, five-sided stems, and then some flat stems like those of *C. phyllanthus*. Kölreuter also gives cases of hybrid Lobelias and Verbascums, which at first produced flowers of one colour, and later in the season, flowers of a different colour.[118] Naudin[119] raised forty hybrids from *Datura lævis* fertilised by *D. stramonium*; and three of these hybrids produced many capsules, of which a half, or quarter, or lesser segment was smooth and of small size, like the capsule of the pure *D. lævis*, the remaining part being spinose and of larger size, like the capsule of the pure *D. stramonium*: from one of these composite capsules, plants perfectly resembling both parent-forms were raised.

Turning now to varieties. A *seedling* apple, conjectured to be of crossed parentage, has been described in France,[120] which bears fruit with one half larger than the other, of a red colour, acid taste, and peculiar odour; the other side being greenish-yellow and very sweet: it is said scarcely ever to include perfectly developed seed. I suppose that this is not the same tree as that which Gaudichaud[121] exhibited before the French institute, bearing on the same branch two distinct kinds of apples, one a *reinette rouge*, and the other like a *reinette canada jaunâtre*: this double-bearing variety can be propagated by grafts, and continues to produce both kinds; its origin is unknown. The Rev. J. D. La Touche sent me a coloured drawing of an apple which he brought from Canada, of which half, surrounding and including the whole of the calyx and the insertion of the foot-stalk, is green, the other half being brown and of the nature of the *pomme gris* apple, with the line of separation between the two

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[116] 'Bastarderzeugung,' s. 549. It is, however, doubtful whether these plants should be ranked as species or varieties.

[117] Gärtner, ibid., s. 550.

[118] 'Journal de Physique,' tom. xxiii., 1873, p. 100. 'Act. Acad. St. Petersburgh,' 1781, part i. p. 249.

[119] 'Nouvelles Archives du Muséum,' tom. i. p. 49.

[120] L'Hermès, Jan. 14, 1837, quoted in Loudon's 'Gard. Mag.,' vol. xiii. p. 230.

[121] 'Comptes Rendus,' tom. xxxiv., 1852, p. 746.

halves exactly defined. The tree was a grafted one, and Mr. La Touche thinks that the branches which bore this curious apple sprung from the point of junction of the graft and stock: had this fact been ascertained, the case would probably have come into the class of graft-hybrids already given. But the branch may have sprung from the stock, which no doubt was a seedling.

Prof. H. Lecoq, who has made a great number of crossings between the differently coloured varieties of *Mirabilis jalapa*,[122] finds that in the seedlings the colours rarely combine, but form distinct stripes; or half the flower is of one colour and half of a different colour. Some varieties regularly bear flowers striped with yellow, white, and red; but plants of such varieties occasionally produce on the same root branches with uniformly coloured flowers of all three tints, and other branches with half-and-half coloured flowers, and others with marbled flowers. Gallesio[123] crossed reciprocally white and red carnations, and the seedlings were striped; but some of the striped plants also bore entirely white and entirely red flowers. Some of these plants produced one year red flowers alone, and in the following year striped flowers; or conversely, some plants, after having borne for two or three years striped flowers, would revert and bear exclusively red flowers. It may be worth mentioning that I fertilised the *Purple Sweet-pea* (*Lathyrus odoratus*) with pollen from the light-coloured *Painted Lady:* seedlings raised from the same pod were not intermediate in character, but perfectly resembled either parent. Later in the summer, the plants which had at first borne flowers identical with those of the *Painted Lady*, produced flowers streaked and blotched with purple; showing in these darker marks a tendency to reversion to the mother-variety. Andrew Knight[124] fertilised two white grapes with pollen of the Aleppo grape, which is darkly variegated both in its leaves and fruit. The result was that the young seedlings were not at first variegated, but all became variegated during the succeeding summer; besides this, many produced on the same plant bunches of grapes which were all black, or all white, or lead-coloured striped with white, or white dotted with minute black stripes; and grapes of all these shades could frequently be found on the same footstalk.

I will append a very curious case, not of bud-variation, but of two cohering embryos, different in character and contained within the same seed. A distinguished botanist, Mr. G. H. Thwaites,[125] states that a seed from *Fuchsia coccinea* fertilised by *F. fulgens*, contained two embryos, and was "a true vegetable twin." The two plants produced from the two embryos were "extremely different in appearance and character," though both resembled other hybrids of the

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[122] 'Géograph. Bot. de l'Europe,' tom. iii., 1854, p. 405; and 'De la Fécondation,' 1862, p. 302.

[123] 'Traité du Citrus,' 1811, p. 45.

[124] 'Transact. Linn. Soc.,' vol. ix. p. 268.

[125] 'Annals and Mag. of Nat. Hist.,' March, 1848.

same parentage produced at the same time. These twin plants "were closely coherent, below the two pairs of cotyledon-leaves, "into a single cylindrical stem, so that they had subsequently the "appearance of being branches on one trunk." Had the two united stems grown up to their full height, instead of dying, a curiously mixed hybrid would have been produced. A mongrel melon described by Sageret[126] may perhaps have thus originated; for the two main branches, which arose from two cotyledon-buds, produced very different fruit,—on the one branch like that of the paternal variety, and on the other branch like to a certain extent that of the maternal variety, the melon of China.

In most of these cases of crossed varieties, and in some of the cases of crossed species, the colours proper to both parents appeared in the seedlings, as soon as they first flowered, in the form of stripes or larger segments, or as whole flowers or fruit of different kinds borne on the same plant; and in this case the appearance of the two colours cannot strictly be said to be due to reversion, but to some incapacity of fusion. When, however, the later flowers or fruit produced during the same season, or during a succeeding year or generation, become striped or half-and-half, &c., the segregation of the two colours is strictly a case of reversion by bud-variation. Whether all the many recorded cases of striped flowers and fruit are due to previous hybridisation and reversion is by no means clear, for instance with peaches and nectarines, moss-roses, &c. In a future chapter I shall show that, with animals of crossed parentage, the same individual has been known to change its character during growth, and to revert to one of its parents which it did not at first resemble. Finally, from the various facts now given, there can be no doubt that the same individual plant, whether a hybrid or a mongrel, sometimes returns in its leaves, flowers, and fruit, either wholly or by segments, to both parent-forms.

On the direct or immediate action of the male element on the mother form.—Another remarkable class of facts must be here considered, firstly, because they have a high physiological importance, and secondly, because they have been supposed to account for some cases of bud-variation. I refer to the direct

[126] 'Pomologie Physiolog.,' 1830, p. 126.

action of the male element, not in the ordinary way on the ovules, but on certain parts of the female plant, or in case of animals on the subsequent progeny of the female by a second male. I may premise that with plants the ovarium and the coats of the ovules are obviously parts of the female, and it could not have been anticipated that they would have been affected by the pollen of a foreign variety or species, although the development of the embryo, inside the embryonic sack, inside the ovule and ovarium, of course, depends on the male element.

Even as long ago as 1729 it was observed[127] that white and blue varieties of the Pea, when planted near each other, mutually crossed, no doubt through the agency of bees, and in the autumn blue and white peas were found within the same pods. Wiegmann made an exactly similar observation in the present century. The same result has followed several times when a variety with peas of one colour has been artificially crossed by a differently-coloured variety.[128] These statements led Gärtner, who was highly sceptical on the subject, carefully to try a long series of experiments: he selected the most constant varieties, and the result conclusively showed that the colour of the skin of the pea is modified when pollen of a differently coloured variety is used. This conclusion has since been confirmed by experiments made by the Rev. J. M. Berkeley.[129]

Mr. Laxton of Stamford, whilst making experiments on peas for the express purpose of ascertaining the influence of foreign pollen on the mother-plant, has recently[130] observed an important additional fact. He fertilised the Tall Sugar-pea, which bears very thin green pods, becoming brownish-white when dry, with pollen of the Purple-podded pea, which, as its name expresses, has dark-purple pods with very thick skin, becoming pale reddish purple when dry. Mr. Laxton has cultivated the tall sugar-pea during twenty years, and has never seen or heard of it producing a purple pod: nevertheless, a flower fertilised by pollen from the purple-pod yielded a pod clouded with purplish-red which Mr. Laxton kindly gave to me. A space of about two inches in length towards the extremity of the pod, and a smaller space near the stalk, were thus coloured. On comparing the colour with that of the purple pod, both pods having been first dried and then soaked in water, it was found to be identically the same; and in both the colour was confined to the cells lying immediately beneath the outer skin of the pod. The valves of the

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[127] 'Philosophical Transact.,' vol. xliii., 1744–45, p. 525.

[128] Mr. Goss, in 'Transact. Hort. Soc.,' vol. v. p. 234: and Gärtner, 'Bastarderzeugung,' 1849, ss. 81 and 499.

[129] 'Gard. Chron.,' 1854, p. 404.

[130] Ibid., 1866, p. 900.

crossed pod were also decidedly thicker and stronger than those of the pods of the mother-plant, but this may possibly have been an accidental circumstance, for I know not how far their thickness is a variable character in the Tall Sugar-pea.

The peas of the Tall Sugar-pea, when dry, are pale greenish-brown, thickly covered with dots of dark purple so minute as to be visible only through a lens, and Mr. Laxton has never seen or heard of this variety producing a purple pea; but in the crossed pod one of the peas was of a uniform beautiful violet-purple tint, and a second was irregularly clouded with pale purple. The colour lies in the outer of the two coats which surround the pea. As the peas of the purple-podded variety when dry are of a pale greenish-buff, it would at first appear that this remarkable change of colour in the peas in the crossed pod could not have been caused by the direct action of the pollen of the purple-pod: but when we bear in mind that this latter variety has purple flowers, purple marks on its stipules, and purple pods; and that the Tall Sugar-pea likewise has purple flowers and stipules, and microscopically minute purple dots on the peas, we can hardly doubt that the tendency to the production of purple in both parents has in combination modified the colour of the peas in the crossed pod. After having examined these specimens, I crossed the same two varieties, and the peas in one pod but not the pods themselves, were clouded and tinted with purplish-red in a much more conspicuous manner than the peas in the uncrossed pods produced at the same time by the same plants. I may notice as a caution that Mr. Laxton sent me various other crossed peas slightly, or even greatly, modified in colour; but the change in these cases was due, as had been suspected by Mr. Laxton, to the altered colour of the cotyledons, seen through the transparent coats of the peas; and as the cotyledons are parts of the embryo, these cases are not in any way remarkable.

Turning now to the genus Matthiola. The pollen of one kind of stock sometimes affects the colour of the seeds of another kind, used as the mother-plant. I give the following case the more readily, as Gärtner doubted similar statements previously made with respect to the stock by other observers. A well-known horticulturist, Major Trevor Clarke, informs me[131] that the seeds of the large red-flowered *biennial* stock, *Matthiola annua* (*Cocardeau* of the French), are light brown, and those of the purple branching Queen stock (*M. incana*) are violet-black; and he found that, when flowers of the red stock were fertilised by pollen from the purple stock, they yielded about fifty per cent. of *black* seeds. He sent me four pods from a red flowered plant, two of which had been fertilised by their own pollen, and they included pale brown seed; and two which had been crossed by pollen from the purple kind, and they included seeds all deeply tinged with black. These latter seeds yielded

[131] *See* also a paper by this observer, read before the International Hort. and Bot. Congress of London, 1866.

purple-flowered plants like their father; whilst the pale brown seeds yielded normal red-flowered plants; and Major Clarke, by sowing similar seeds, has observed on a greater scale the same result. The evidence in this case of the direct action of the pollen of one species on the colour of the seeds of another species appears to me conclusive.

Gallesio[132] fertilised the flowers of an orange with pollen from the lemon; and one fruit thus produced bore a longitudinal stripe of peel having the colour, flavour, and other characters of the lemon. Mr. Anderson[133] fertilised a green-fleshed melon with pollen from a scarlet-fleshed kind; in two of the fruits "a sensible change was perceptible: and four other fruits were somewhat altered both internally and externally." The seeds of the two first-mentioned fruits produced plants partaking of the good properties of both parents. In the United States, where Cucurbitaceæ are largely cultivated, it is the popular belief[134] that the fruit is thus directly affected by foreign pollen; and I have received a similar statement with respect to the cucumber in England. It is believed that grapes have been thus affected in colour, size, and shape: in France a pale-coloured grape had its juice tinted by the pollen of the dark-coloured Teinturier; in Germany a variety bore berries which were affected by the pollen of two adjoining kinds; some of the berries being only partially affected or mottled.[135]

As long ago as 1751[136] it was observed that, when differently-coloured varieties of maize grew near each other, they mutually affected each other's seeds, and this is now a popular belief in the United States. Dr. Savi[137] tried the experiment with care: he sowed yellow and black-seeded maize together, and on the same ear some of the seeds were yellow, some black, and some mottled, the differently coloured seeds being arranged irregularly or in rows. Prof. Hildebrand has repeated the experiment[138] with the precaution of ascertaining that the mother-plant was true. A kind bearing yellow grains was fertilised with pollen of a kind having brown grains, and two ears produced yellow grains mingled with others of a dirty violet tint. A third ear had only yellow grains, but one side of the spindle was tinted of a reddish-brown; so that here we have the important fact of the influence of the foreign pollen extending

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[132] 'Traité du Citrus,' p. 40.

[133] 'Transact. Hort. Soc.,' vol. iii. p. 318. *See* also vol. v. p. 65.

[134] Prof. Asa Gray, 'Proc. Acad. Sc.,' Boston, vol. iv., 1860, p. 21. I have received statements to the same effect from other persons in the United States.

[135] For the French case, *see* 'Journ. Hort. Soc.,' vol. i. new series, 1866, p. 50. For Germany, *see* M. Jack, quoted in Henfrey's 'Botanical Gazette,' vol. i. p. 277. A case in England has recently been alluded to by the Rev. J. M. Berkeley before the Hort. Soc. of London.

[136] 'Philosophical Transactions,' vol. xlvii., 1751–52, p. 206.

[137] Gallesio, 'Teoria della Riproduzione,' 1816, p. 95.

[138] 'Bot. Zeitung,' May, 1868, p. 326.

to the axis. Mr. Arnold, in Canada, varied the experiment in an interesting manner: "a female flower was subjected first to the "action of pollen from a yellow variety, and then to that from a "white variety; the result was an ear, each grain of which was "yellow below and white above."[139] With other plants it has occasionally been observed that the crossed offspring showed the influence of two kinds of pollen, but in this case the two kinds affected the mother-plant.

Mr. Sabine states[140] that he has seen the form of the nearly globular seed-capsule of *Amaryllis vittata* altered by the application of the pollen of another species, of which the capsule has gibbous angles. With an allied genus, a well-known botanist, Maximowicz, has described in detail the striking results of reciprocally fertilising *Lilium bulbiferum* and *davuricum* with each other's pollen. Each species produced fruit not like its own, but almost identical with that of the pollen-bearing species; but from an accident only the fruit of the latter species was carefully examined; the seeds were intermediate in the development of their wings.[141]

Fritz Müller fertilised *Cattleya leopoldi* with pollen of *Epidendron cinnabarinum*; and the capsules contained very few seeds; but these presented a most wonderful appearance, which, from the description given, two botanists, Hildebrand and Maximowicz, attribute to the direct action of the pollen of the Epidendron.[142]

Mr. J. Anderson Henry[143] crossed *Rhododendron dalhousiæ* with the pollen of *R. nuttallii*, which is one of the largest-flowered and noblest species of the genus. The largest pod produced by the former species, when fertilised with its own pollen, measured $1\frac{2}{3}$ inch in length and $1\frac{1}{2}$ in girth; whilst three of the pods which had been fertilised by pollen of *R. nuttallii* measured $1\frac{5}{8}$ inch in length and no less than 2 inches in girth. Here the effect of the foreign pollen was apparently confined to increasing the size of the ovarium; but we must be cautious in assuming, as the following case shows, that size had been transferred from the male parent to the capsule of the female plant. Mr. Henry fertilised *Arabis blepharophylla* with pollen of *A. soyeri*, and the pods thus produced, of which he was so kind as to send me detailed measurements and sketches, were much larger in all their dimensions than those naturally produced by either the male or female parent-species. In a future chapter we shall see that the organs of vegetation in hybrid plants, indepen-

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[139] *See* Dr. J. Stockton-Hough, in American Naturalist,' Jan. 1874, p. 29.

[140] 'Transact. Hort. Soc.,' vol. v. p. 69.

[141] 'Bull. de l'Acad. Imp. de St. Petersburg,' tom. xvii. p. 275, 1872. The author gives references to those cases in the Solanaceæ of fruit affected by foreign pollen, but as it does not appear that the mother-plant was artificially fertilised, I have not entered into details.

[142] "Bot. Zeitung,' Sept. 1868, p. 631. For Maximowicz's judgment, see the paper last referred to.

[143] 'Journal of Horticulture,' Jan. 20, 1863, p. 46.

dently of the character of either parent, are sometimes developed to a monstrous size; and the increased size of the pods in the foregoing cases may be an analogous fact. On the other hand, M. de Saporta informs me that an isolated female plant of *Pistacia vera* is very apt to be fertilised by the pollen of neighbouring plants of *P. terebinthus*, and in this case the fruits are only half their proper size, which he attributes to the influence of the pollen of *P. terebinthus*.

No case of the direct action of the pollen of one variety on another is better authenticated or more remarkable than that of the common apple. The fruit here consists of the lower part of the calyx and of the upper part of the flower-peduncle[144] in a metamorphosed condition, so that the effect of the foreign pollen has extended even beyond the limits of the ovarium. Cases of apples thus affected were recorded by Bradley in the early part of the last century; and other cases are given in old volumes of the 'Philosophical Transactions;'[145] in one of these a Russeting apple and an adjoining kind mutually affected each other's fruit; and in another case a smooth apple affected a rough-coated kind. Another instance has been given[146] of two very different apple-trees growing close to each other, which bore fruit resembling each other, but only on the adjoining branches. It is, however, almost superfluous to adduce these or other cases, after that of the St. Valery apple, the flowers which, from the abortion of the stamens, do not produce pollen, but are fertilised by the girls of the neighbourhood with pollen of many kinds; and they bear fruit, "differing from one another in size, flavour, and colour, but resembling in character the hermaphrodite kinds by which they have been fertilised."[147]

I have now shown, on the authority of several excellent observers, in the case of plants belonging to widely different orders, that the pollen of one species or variety, when applied to the female of a distinct form, occasionally causes the coats of the seeds, the ovarium or fruit, including even the calyx and upper part of the peduncle of the apple, and the axis of the ear in maize, to be modified. Sometimes the whole ovarium or all the seeds are thus affected; sometimes only a

[144] *See* on this head the high authority of Prof. Decaisne, in a paper translated in 'Journ. Hort. Soc.,' vol. i., new series, 1866, p. 48.

[145] Vol. xliii., 1744–45, p. 525; vol. xlv., 1747–48, p. 602.

[146] 'Transact. Hort. Soc.,' vol. v. pp. 65 and 68. *See*, also, Prof. Hildebrand, with a coloured figure, in 'Bot. Zeitung,' May 15, 1868, p. 327. Puvis also has collected, 'De la Dégénération,' 1837, p. 36) several other instances; but it is not in all cases possible to distinguish between the direct action of foreign pollen and bud-variations.

[147] T. de Clermont-Tonnerre, in 'Mém. de la Soc. Linn. de Paris,' tom. iii., 1825, p. 164.

certain number of the seeds, as in the case of the pea, or only a part of the ovarium, as with the striped orange, mottled grapes, and maize, is thus affected. It must not be supposed that any direct or immediate effect invariably follows the use of foreign pollen: this is far from being the case; nor is it known on what conditions the result depends. Mr. Knight[148] expressly states that he has never seen the fruit thus affected, though he crossed thousands of apple and other fruit-trees.

There is not the least reason to believe that a branch which has borne seed or fruit directly modified by foreign pollen is itself affected, so as afterwards to produce modified buds; such an occurrence, from the temporary connection of the flower with the stem, would be hardly possible. Hence, but very few, if any, of the cases of bud-variation in the fruit of trees, given in the early part of this chapter can be accounted for by the action of foreign pollen; for such fruits have commonly been propagated by budding or grafting. It is also obvious that changes of colour in flowers, which necessarily supervene long before they are ready for fertilisation, and changes in the shape or colour of leaves, when due to the appearance of modified buds, can have no relation to the action of foreign pollen.

The proofs of the action of foreign pollen on the mother-plant have been given in considerable detail, because this action, as we shall see in a future chapter, is of the highest theoretical importance, and because it is in itself a remarkable and apparently anomalous circumstance. That it is remarkable under a physiological point of view is clear, for the male element not only affects, in accordance with its proper function, the germ, but at the same time various parts of the mother-plant, in the same manner, as it affects the same part in the seminal offspring from the same two parents. We thus learn that an ovule is not indispensable for the reception of the influence of the male element. But this direct action of the male element is not so anomalous as it at first appears, for it comes into play in the ordinary fertilisation of many

[148] 'Transact. of Hort. Soc.,' vol. v. p. 68.

flowers. Gärtner gradually increased the number of pollen grains until he succeeded in fertilising a Malva, and has[147] proved that many grains are first expended in the development, or, as he expresses it, in the satiation, of the pistil and ovarium. Again, when one plant is fertilised by a widely distinct species, it often happens that the ovarium is fully and quickly developed without any seeds being formed; or the coats of the seeds are formed without any embryo being developed within. Prof. Hildebrand, also, has lately shown[148] that, in the normal fertilisation of several Orchideæ, the action of the plant's own pollen is necessary for the development of the ovarium; and that this development takes place not only long before the pollen-tubes have reached the ovules, but even before the placentæ and ovules have been formed; so that with these orchids the pollen acts directly on the ovarium. On the other hand, we must not overrate the efficacy of pollen in the case of hybridised plants, for an embryo may be formed and its influence excite the surrounding tissues of the mother-plant, and then perish at a very early age and be thus overlooked. Again, it is well known that with many plants the ovarium may be fully developed, though pollen be wholly excluded. Lastly, Mr. Smith, the late Curator at Kew (as I hear through Dr. Hooker), observed with an orchid, the *Bonatea speciosa*, the singular fact that the development of the ovarium could be effected by the mechanical irritation of the stigma. Nevertheless, from the number of the pollen-grains expended "in the satiation of the ovarium and pistil,"—from the generality of the formation of the ovarium and seed-coats in hybridised plants which produce no seeds,—and from Dr. Hildebrand's observations on orchids, we may admit that in most cases the swelling of the ovarium, and the formation of the seed-coats are at least aided, if not wholly caused, by the direct action of the pollen, independently of the intervention of the fertilised germ. Therefore, in the previously given cases we have only to

[149] 'Beiträge zur Kenntniss der Befruchtung,' 1844, s. 347–351.

[150] 'Die Fruchtbildung der Orchideen, ein Beweis für die doppelte Wirkung des Pollens,' 'Botanische Zeitung,' No. 44 et seq., Oct. 30, 1865; and Aug. 4, 1865, s. 249.

believe in the further power of pollen, when applied to a distinct species or variety, to influence the shape, size, colour, texture, &c., of certain parts of the mother-plant.

Turning now to the animal kingdom. If we could imagine the same flower to yield seeds during successive years, then it would not be very surprising that a flower of which the ovarium had been modified by foreign pollen should next year produce, when self-fertilised, offspring modified by the previous male influence. Closely analogous cases have actually occurred with animals. In the case often quoted from Lord Morton,[151] a nearly purely-bred Arabian chesnut mare bore a hybrid to a quagga; she was subsequently sent to Sir Gore Ouseley, and produced two colts by a black Arabian horse. These colts were partially dun-coloured, and were striped on the legs more plainly than the real hybrid, or even than the quagga. One of the two colts had its neck and some other parts of its body plainly marked with stripes. Stripes on the body, not to mention those on the legs, are extremely rare,—I speak after having long attended to the subject,—with horses of all kinds in Europe, and are almost unknown in the case of Arabians. But what makes the case still more striking is that in these colts the hair of the mane resembled that of the quagga, being short, stiff, and upright. Hence there can be no doubt that the quagga affected the character of the offspring subsequently begot by the black Arabian horse. Mr. Jenner Weir informs me of a strictly parallel case: his neighbour Mr. Lethbridge, of Blackheath, has a horse, bred by Lord Mostyn, which had previously borne a foal by a quagga. This horse is dun with a dark stripe down the back, faint stripes on the forehead between the eyes, plain stripes on the inner side of the fore-legs and rather more faint ones on the hind-legs, with no shoulder-stripe. The mane grows much lower on the forehead than in the horse, but not so low as in the quagga or zebra. The hoofs are proportionally longer than in the horse,—so much so that the farrier who first shod this animal, and knew nothing of

[151] 'Philos. Transact.,' 1821, p. 20.

its origin, said, "Had I not seen I was shoeing a horse, I should have thought I was shoeing a donkey."

With respect to the varieties of our domesticated animals, many similar and well-authenticated facts have been published,[152] and others have been communicated to me, plainly showing the influence of the first male on the progeny subsequently borne by the mother to other males. It will suffice to give a single instance, recorded in the 'Philosophical Transactions,' in a paper following that by Lord Morton: Mr. Giles put a sow of Lord Western's black and white Essex breed to a wild boar of a deep chesnut colour; and the "pigs produced partook in appearance of both boar and sow, but in some the chesnut colour of the boar strongly prevailed." After the boar had long been dead, the sow was put to a boar of her own black and white breed—a kind

[152] Dr. Alex. Harvey on 'A remarkable Effect of Cross-breeding,' 1851. On the 'Physiology of Breeding,' by Mr. Reginald Orton, 1855. 'Intermarriage,' by Alex. Walker, 1837. 'L'Hérédité Naturelle,' by Dr. Prosper Lucas, tom. ii. p. 58. Mr. W. Sedgwick in 'British and Foreign Medico-Chirurgical Review,' 1863, July, p. 183. Bronn, in his 'Geschichte der Natur,' 1843, B. ii. s. 127, has collected several cases with respect to mares, sows, and dogs. Mr. W. C. L. Martin ('History of the Dog,' 1845, p. 104) says he can personally vouch for the influence of the male parent on subsequent *litters by other dogs*. A French poet, Jacques Savary, who wrote in 1665 on dogs, was aware of this singular fact. Dr. Bowerbank has given us the following striking case:—A black, hairless Barbary bitch was first accidentally impregnated by a mongrel spaniel with long brown hair, and she produced five puppies, three of which were hairless and two covered with *short* brown hair. The next time she was put to a black, hairless Barbary dog; "but the mischief had been implanted in the mother, and again about half the litter looked like pure Barbarys, and the other half like the *short*-haired progeny of the first father." I have given in the text one case with pigs; an equally striking one has been recently published in Germany, 'Illust. Landwirth. Zeitung,' 1868, Nov. 17, p. 143. It is worth notice that farmers in S. Brazil (as I hear from Fritz Müller), and at the C. of Good Hope (as I have heard from two trustworthy persons) are convinced that mares which have once borne mules, when subsequently put to horses, are extremely liable to produce colts, striped like a mule. Dr. Wilckens, of Pogarth, gives ('Jahrbuch Landwirthschaft,' ii. 1869, p. 325) a striking and analogous case. A merino ram, having two small lappets or flaps of skin on the neck, was in the winter of 1861–62 put to several Merino ewes, all of whom bore lambs with similar flaps on their necks. The ram was killed in the spring of 1862, and subsequently to his death the ewes were put to other Merino rams, and in 1863 to Southdown rams, none of whom ever have neck lappets: nevertheless, even as long afterwards as 1867, several of these ewes produced lambs bearing these appendages.

which is well known to breed very true and never to show any chesnut colour,—yet from this union the sow produced some young pigs which were plainly marked with the same chesnut tint as in the first litter. Similar cases have so frequently occurred, that careful breeders avoid putting a choice female of any animal to an inferior male, on account of the injury to her subsequent progeny which may be expected to follow.

Some physiologists have attempted to account for these remarkable results from a previous impregnation, by the imagination of the mother having been strongly affected; but it will hereafter be seen that there are very slight grounds for any such belief. Other physiologists attribute the result to the close attachment and freely intercommunicating blood-vessels between the modified embryo and mother. But the analogy from the action of foreign pollen on the ovarium, seed-coats, and other parts of the mother-plant, strongly supports the belief that with animals the male element acts directly on the female, and not through the crossed embryo. With birds there is no close connection between the embryo and mother; yet a careful observer, Dr. Chapuis, states[153] that with pigeons the influence of a first male sometimes makes itself perceived in the succeeding broods; but this statement requires confirmation.

Conclusion and Summary of the Chapter.—The facts given in the latter half of this chapter are well worthy of consideration, as they show us in how many extraordinary modes the union of one form with another may lead to the modification of the seminal offspring or of the buds, afterwards produced.

There is nothing surprising in the offspring of species or varieties crossed in the ordinary manner being modified; but the case of two plants within the same seed, which cohere and differ from each other, is curious. When a bud is formed after the cellular tissue of two species or two varieties have been united, and it partakes of the characters of both parents, the case is wonderful. But I need not here repeat what has been so lately said on this subject. We have

[153] 'Le Pigeon Voyageur Belge,' 1865, p. 59.

also seen that in the case of plants the male element may affect in a direct manner the tissues of the mother, and with animals may lead to the modification of her future progeny. In the vegetable kingdom the offspring from a cross between two species or varieties, whether effected by seminal generation or by grafting, often revert, to a greater or less degree, in the first or in a succeeding generation, to the two parent-forms; and this reversion may affect the whole flower, fruit, or leaf-bud, or only the half or a smaller segment of a single organ. In some cases, however, such segregation of character apparently depends on an incapacity for union rather than on reversion, for the flowers or fruit which are first produced display by segments the characters of both parents. The various facts here given ought to be well considered by any one who wishes to embrace under a single point of view the many modes of reproduction by gemmation, division, and sexual union, the reparation of lost parts, variation, inheritance, reversion, and other such phenomena. Towards the close of the second volume I shall attempt to connect these facts together by the hypothesis of pangenesis.

In the early half of the present chapter I have given a long list of plants in which through bud-variation, that is, independently of reproduction by seed, the fruit has suddenly become modified in size, colour, flavour, hairiness, shape, and time of maturity; flowers have similarly changed in shape, colour, in being double, and greatly in the character of the calyx; young branches or shoots have changed in colour, in bearing spines and in habit of growth, as in climbing or in weeping; leaves have changed in becoming variegated, in shape, period of unfolding, and in their arrangement on the axis. Buds of all kinds, whether produced on ordinary branches or on subterranean stems, whether simple or much modified and supplied with a stock of nutriment, as in tubers and bulbs, are all liable to sudden variations of the same general nature.

In the list, many of the cases are certainly due to reversion to characters not acquired from a cross, but which were formerly present and have since been lost for a longer or shorter time;—as when a bud on a variegated plant produces plain leaves, or when the variously-coloured flowers of the

Chrysanthemum revert to the aboriginal yellow tint. Many other cases included in the list are probably due to the plants being of crossed parentage, and to the buds reverting either completely or by segments to one of the two parent-forms.[154]

We may suspect that the strong tendency in the Chrysanthemum to produce by bud-variation differently-coloured flowers, results from the varieties having been at some time intentionally or accidentally crossed; and this is certainly the case with some kinds of Pelargonium. So it may be to a large extent with the bud-varieties of the Dahlia, and with the "broken colours" of Tulips. When, however, a plant reverts by bud-variation to its two parent forms, or to one of them, it sometimes does not revert perfectly, but assumes a somewhat new character,—of which fact, instances have been given, and Carrière gives[155] another in the cherry.

Many cases of bud-variation, however, cannot be attributed to reversion, but to so-called spontaneous variability, as is so common with cultivated plants raised from seed. As a single variety of the Chrysanthemum has produced by buds six other varieties, and as one variety of the gooseberry has borne at the same time four distinct kinds of fruit, it is scarcely possible to believe that all these variations are due to reversion. We can hardly believe, as remarked in a previous chapter, that all the many peaches which have yielded nectarine-buds are of crossed parentage. Lastly, in such cases as that of the moss-rose, with its peculiar calyx, and of the rose which bears opposite leaves, in that of the Imantophyllum, &c., there is no known natural species or variety

[154] It may be worth while to call attention to the several means by which flowers and fruit become striped or mottled. Firstly, by the direct action of the pollen of another variety or species, as in the cases given of oranges and maize. Secondly, in crosses of the first generation, when the colours of the two parents do not readily unite, as with Mirabilis and Dianthus. Thirdly, in crossed plants of a subsequent generation by reversion, through either bud or seminal generation. Fourthly, by reversion to a character not originally gained by a cross, but which had long been lost, as with white-flowered varieties, which we shall hereafter see often become striped with some other colour. Lastly, there are cases, as when peaches are produced with a half or quarter of the fruit like a nectarine, in which the change is apparently due to mere variation, through either bud or seminal generation.

[155] 'Production des Variétés, p. 37.

from which the characters in question could have been derived by a cross. We must attribute all such cases to the appearance of absolutely new characters in the buds. The varieties which have thus arisen cannot be distinguished by any external character from seedlings; this is notoriously the case with the varieties of the Rose, Azalea, and many other plants. It deserves notice that all the plants which have yielded bud-variations have likewise varied greatly by seed.

The plants which have varied by buds belong to so many orders that we may infer that almost every plant would be liable to variation, if placed under the proper exciting conditions. These conditions, as far as we can judge, mainly depend on long-continued and high cultivation; for almost all the plants in the foregoing list are perennials, and have been largely propagated in many soils, under different climates, by cuttings, offsets, bulbs, tubers, and especially by budding or grafting. The instances of annuals varying by buds, or producing on the same plant differently coloured flowers, are comparatively rare: Hopkirk [156] has seen this with *Convolvulus tricolor*; and it is not uncommon with the Balsam and annual Delphinium. According to Sir R. Schomburgk, plants from the warmer temperate regions, when cultivated under the hot climate of St. Domingo, are eminently liable to bud-variation. I am informed by Mr. Sedgwick that moss-roses which have often been taken to Calcutta always there lose their mossiness; but change of climate is by no means a necessary contingent, as we see with the gooseberry, currant, and in many other cases. Plants living under their natural conditions are very rarely subject to bud-variation. Variegated leaves have, however, been observed under such circumstances; and I have given an instance of variation by buds on an ash-tree planted in ornamental grounds, but it is doubtful whether such a tree can be considered as living under strictly natural conditions. Gärtner has seen white and dark-red flowers produced from the same root of the wild *Achillea millefolium*; and Prof. Caspary has seen a completely wild *Viola lutea* bearing flowers of two different colours and sizes.[157]

[156] 'Flora Anomala,' p. 164.

[157] 'Schriften der physisch-okon. Gesell. zu Königsberg,' Band vi., Feb 3, 1865, s. 4.

As wild plants are so rarely liable to bud-variation, whilst highly cultivated plants long propagated by artificial means have yielded many varieties by this form of reproduction, we are led through a series such as the following,—namely, all the eyes in the same tuber of the potato varying in the same manner,—all the fruit on a purple plum-tree suddenly becoming yellow,—all the fruit on a double-flowered almond suddenly becoming peach like,—all the buds on grafted trees being in a very slight degree affected by the stock on which they have been worked,—all the flowers on a transplanted heartsease changing for a time in colour, size, and shape,—we are led by such a series to look at every case of bud-variation as the direct result of the conditions of life to which the plant has been exposed. On the other hand, plants of the same variety may be cultivated in two adjoining beds, apparently under exactly the same conditions, and those in the one bed, as Carrière insists,[158] will produce many bud-variations, and those in the other not a single one. Again, if we look to such cases as that of a peach-tree which, after having been cultivated by tens of thousands during many years in many countries, and after having annually produced millions of buds, all of which have apparently been exposed to precisely the same conditions, yet at last suddenly produces a single bud with its whole character greatly transformed, we are driven to the conclusion that the transformation stands in no *direct* relation to the conditions of life.

We have seen that varieties produced from seeds and from buds resemble each other so closely in general appearance that they cannot be distinguished. Just as certain species and groups of species, when propagated by seed, are more variable than other species or genera, so it is in the case of certain bud-varieties. Thus, the Queen of England Chrysanthemum has produced by this latter process no less than six, and Rollisson's Unique Pelargonium four distinct varieties; moss-roses have also produced several other moss-roses. The Rosaceæ have varied by buds more than any other group of plants; but this may be in large part due to so many members having been long cultivated; but

[158] 'Production des Variétés,' pp. 58, 70.

within this same group, the peach has often varied by buds, whilst the apple and pear, both grafted trees extensively cultivated, have afforded, as far as I can ascertain, extremely few instances of bud-variation.

The law of analogous variation holds good with varieties produced by buds, as with those produced from seed: more than one kind of rose has sported into a moss-rose; more than one kind of camellia has assumed an hexagonal form; and at least seven or eight varieties of the peach have produced nectarines.

The laws of inheritance seem to be nearly the same with seminal and bud-varieties. We know how commonly reversion comes into play with both, and it may affect the whole, or only segments of a leaf, flower, or fruit. When the tendency to reversion affects many buds on the same tree, it becomes covered with different kinds of leaves, flowers, or fruit; but there is reason to believe that such fluctuating varieties have generally arisen from seed. It is well known that, out of a number of seedling varieties, some transmit their character much more truly by seed than others; so with bud-varieties, some retain their character by successive buds more truly than others; of which instances have been given with two kinds of variegated Euonymus and with certain kinds of tulips and pelargoniums. Notwithstanding the sudden production of bud-varieties, the characters thus acquired are sometimes capable of transmission by seminal reproduction: Mr. Rivers has found that moss-roses generally reproduce themselves by seed; and the mossy character has been transferred by crossing from one species of rose to another. The Boston nectarine, which appeared as a bud-variation, produced by seed a closely allied nectarine. On the other hand, seedlings from some bud-variations have proved variable to an extreme degree.[157] We have also heard, on the authority of Mr. Salter, that seeds taken from a branch with leaves variegated through bud-variation, transmit this character very feebly; whilst many plants, which were variegated as seedlings, transmit variegation to a large proportion of their progeny.

Although I have been able to collect a good many cases of

[159] Carrière, 'Production des Variétés,' p. 39.

bud-variation, as shown in the previous lists, and might probably, by searching foreign horticultural works, have collected very many more cases, yet their total number is as nothing in comparison with that of seminal varieties. With seedlings raised from the more variable cultivated plants, the variations are almost infinitely numerous, but their differences are generally slight: only at long intervals of time a strongly marked modification appears. On the other hand, it is a singular and inexplicable fact that, when plants vary by buds, the variations, though they occur with comparative rarity, are often, or even generally, strongly pronounced. It struck me that this might perhaps be a delusion, and that slight changes often occurred in buds, but were overlooked or not recorded from being of no value. Accordingly, I applied to two great authorities on this subject, namely, to Mr. Rivers with respect to fruit-trees, and to Mr. Salter with respect to flowers. Mr. Rivers is doubtful, but does not remember having noticed very slight variations in fruit-buds. Mr. Salter informs me that with flowers such do occur, but, if propagated, they generally lose their new character in the following year; yet he concurs with me that bud-variations usually at once assume a decided and permanent character. We can hardly doubt that this is the rule, when we reflect on such cases as that of the peach, which has been so carefully observed, and of which such trifling seminal varieties have been propagated, yet this tree has repeatedly produced by bud-variation nectarines, and only twice (as far as I can learn) any other variety, namely, the Early and Late Grosse Mignonne peaches; and these differ from the parent-tree in hardly any character except the period of maturity.

To my surprise, I hear from Mr. Salter that he brings the principle of selection to bear on variegated plants propagated by buds, and has thus greatly improved and fixed several varieties. He informs me that at first a branch often produces variegated leaves on one side alone, and that the leaves are marked only with an irregular edging or with a few lines of white and yellow. To improve and fix such varieties, he finds it necessary to encourage the buds at the bases of the most distinctly marked leaves, and to propagate from them

alone. By following with perseverance this plan during three or four successive seasons, a distinct and fixed variety can generally be secured.

Finally, the facts given in this chapter prove in how close and remarkable a manner the germ of a fertilised seed and the small cellular mass forming a bud, resemble each other in all their functions—in their power of inheritance with occasional reversion,—and in their capacity for variation of the same general nature, in obedience to the same laws. This resemblance, or rather identity of character, is shown in the most striking manner by the fact that the cellular tissue of one species or variety, when budded or grafted on another, may give rise to a bud having an intermediate character. We have seen that variability does not depend on sexual generation, though much more frequently its concomitant than of bud reproduction. We have seen that bud-variability is not solely dependent on reversion or atavism to long-lost characters, or to those formerly acquired from a cross, but appears often to be spontaneous. But when we ask ourselves what is the cause of any particular bud-variation, we are lost in doubt, being driven in some cases to look to the direct action of the external conditions of life as sufficient, and in other cases to feel a profound conviction that these have played a quite subordinate part, of not more importance than the nature of the spark which ignites a mass of combustible matter.