CHAPTER XXVII.

PROVISIONAL HYPOTHESIS OF PANGENESIS.

PRELIMINARY REMARKS—FIRST PART:—THE FACTS TO BE CONNECTED UNDER A SINGLE POINT OF VIEW, NAMELY, THE VARIOUS KINDS OF REPRODUCTION—RE-GROWTH OF AMPUTATED PARTS—GRAFT-HYBRIDS—THE DIRECT ACTION OF THE MALE ELEMENT ON THE FEMALE—DEVELOPMENT—THE FUNCTIONAL INDEPENDENCE OF THE UNITS OF THE BODY—VARIABILITY—INHERITANCE—REVERSION.

SECOND PART:—STATEMENT OF THE HYPOTHESIS—HOW FAR THE NECESSARY ASSUMPTIONS ARE IMPROBABLE—EXPLANATION BY AID OF THE HYPOTHESIS OF THE SEVERAL CLASSES OF FACTS SPECIFIED IN THE FIRST PART—CONCLUSION.

IN the previous chapters large classes of facts, such as those bearing on bud-variation, the various forms of inheritance, the causes and laws of variation, have been discussed; and it is obvious that these subjects, as well as the several modes of reproduction, stand in some sort of relation to one another. I have been led, or rather forced, to form a view which to a certain extent connects these facts by a tangible method. Every one would wish to explain to himself, even in an imperfect manner, how it is possible for a character possessed by some remote ancestor suddenly to reappear in the offspring; how the effects of increased or decreased use of a limb can be transmitted to the child; how the male sexual element can act not solely on the ovules, but occasionally on the mother-form; how a hybrid can be produced by the union of the cellular tissue of two plants independently of the organs of generation; how a limb can be reproduced on the exact line of amputation, with neither too much nor too little added; how the same organism may be produced by such widely different processes, as budding and true seminal generation; and, lastly, how of two allied forms, one passes in the course of its development through the most complex metamorphoses, and the other does not do so, though when mature both are alike in every detail of structure. I am aware that my view is merely a provisional hypothesis or speculation; but until a better one be advanced, it will serve to bring together a multitude of facts which are at present left disconnected by any efficient cause. As Whewell, the historian of the inductive sciences, remarks:—"Hypotheses may often be of service to "science, when they involve a certain portion of incompleteness, and even of error." Under this point of view I venture to advance the hypothesis of Pangenesis, which implies that every separate part of the whole organisation reproduces itself. So that ovules, spermatozoa, and pollen-grains,—the fertilised egg or seed, as well as buds,—include and consist of a multitude of germs thrown off from each separate part or unit.[1]

In the First Part I will enumerate as briefly as I can the groups of facts which seem to demand connection; but certain

[1] This hypothesis has been severely criticised by many writers, and it will be fair to give references to the more important articles. The best essay which I have seen is by Prof. Delpino, entitled 'Sulla Darwiniana Teoria della Pangenesi, 1869,' of which a translation appeared in 'Scientific Opinion,' Sept. 29, 1869 and the succeeding numbers. He rejects the hypothesis, but criticises it fairly, and I have found his criticisms very useful. Mr. Mivart ('Genesis of Species,' 1871, chap. x.) follows Delpino, but adds no new objections of any weight. Dr. Bastian ('The Beginnings of Life,' 1872, vol. ii. p. 98) says that the hypothesis "looks "like a relic of the old rather than a "fitting appanage of the new evolu-"tion philosophy." He shows that I ought not to have used the term "pangenesis," as it had been previously used by Dr. Gros in another sense. Dr. Lionel Beale ('Nature,' May 11, 1871, p. 26) sneers at the whole doctrine with much acerbity and some justice. Prof. Wigand ('Schriften der Gesell. der gesammt. Naturwissen. zu Marburg,' Bd. ix., 1870) considers the hypothesis as unscientific and worthless. Mr. G. H. Lewes ('Fortnightly Review,' Nov. 1, 1868, p. 503) seems to consider that it may be useful: he makes many good criticisms in a perfectly fair spirit. Mr. F. Galton, after describing his valuable experiments ('Proc. Royal Soc.' vol. xix. p. 393) on the intertransfusion of the blood of distinct varieties of the rabbit, concludes by saying that in his opinion the results negative beyond all doubt the doctrine of Pangenesis. He informs me that subsequently to the publication of his paper he continued his experiments on a still larger scale for two more generations, without any sign of mongrelism showing itself in the very numerous offspring. I certainly should have expected that gemmules would have been present in the blood, but this is no necessary part of the hypothesis, which manifestly applies to plants and the lowest animals. Mr. Galton, in a letter to 'Nature' (April 27, 1871, p. 502), also criticises various incorrect expressions used by me. On the other hand, several writers have spoken favourably of the hypothesis, but there would be no use in giving references to their articles. I may, however, refer to Dr. Ross' work, 'The Graft Theory of Disease; being an application of Mr. Darwin's hypothesis of Pangenesis,' 1872, as he gives several original and ingenious discussions.

subjects, not hitherto discussed, must be treated at disproportionate length. In the Second Part the hypothesis will be given; and after considering how far the necessary assumptions are in themselves improbable, we shall see whether it serves to bring under a single point of view the various facts.

PART I.

Reproduction may be divided into two main classes, namely, sexual and asexual. The latter is effected in many ways—by the formation of buds of various kinds, and by fissiparous generation, that is by spontaneous or artificial division. It is notorious that some of the lower animals, when cut into many pieces, reproduce so many perfect individuals: Lyonnet cut a Nais or freshwater worm into nearly forty pieces, and these all reproduced perfect animals.[2] It is probable that segmentation could be carried much further in some of the protozoa; and with some of the lowest plants each cell will reproduce the parent-form. Johannes Müller thought that there was an important distinction between gemmation and fission; for in the latter case the divided portion, however small, is more fully developed than a bud, which also is a younger formation; but most physiologists are now convinced that the two processes are essentially alike.[3] Prof. Huxley remarks, "fission is little "more than a peculiar mode of budding," and Prof. H. J. Clark shows in detail that there is sometimes "a compro-"mise between self-division and budding." When a limb is amputated, or when the whole body is bisected, the cut extremities are said to bud forth;[4] and as the papilla, which is first formed, consists of undeveloped cellular tissue like that forming an ordinary bud, the expression is apparently correct. We see the connection of the two processes in

[2] Quoted by Paget, 'Lectures on Pathology,' 1853, p. 159.

[3] Dr. Lachmann, also, observes ('Annals and Mag. of Nat. History,' 2nd series, vol. xix., 1857, p. 231) with respect to infusoria, that "fissa-"tion and gemmation pass into each "other almost imperceptibly." Again, Mr. W. C. Minor ('Annals and Mag. of Nat. Hist.,' 3rd series, vol. xi. p. 328) shows that with Annelids the distinction that has been made between fission and budding is not a fundamental one. *See*, also, Professor Clark's work, 'Mind in Nature,' New York, 1865, pp. 62, 94.

[4] *See* Bonnet. 'Œuvres d'Hist. Nat.,' tom. v., 1781, p. 339, for remarks on the budding-out of the amputated limbs of Salamanders.

another way; for Trembley observed with the hydra, that the reproduction of the head after amputation was checked as soon as the animal put forth reproductive gemmæ.[5]

Between the production, by fissiparous generation, of two or more complete individuals, and the repair of even a very slight injury, there is so perfect a gradation, that it is impossible to doubt that the two processes are connected. As at each stage of growth an amputated part is replaced by one in the same state of development, we must also follow Sir J. Paget in admitting, "that the powers of development from the "embryo, are identical with those exercised for the restora-"tion from injuries: in other words, that the powers are the "same by which perfection is first achieved, and by which, "when lost, it is recovered."[6] Finally, we may conclude that the several forms of budding, fissiparous generation, the repair of injuries, and development, are all essentially the results of one and the same power.

Sexual Generation.—The union of the two sexual elements seems at first sight to make a broad distinction between sexual and asexual generation. But the conjugation of algæ, by which process the contents of two cells unite into a single mass capable of development, apparently gives us the first step towards sexual union: and Pringsheim, in his memoir on the pairing of Zoospores,[7] shows that conjugation graduates into true sexual reproduction. Moreover, the now well-ascertained cases of Parthenogenesis prove that the distinction between sexual and asexual generation is not nearly so great as was formerly thought; for ova occasionally, and even in some cases *frequently, become developed into* perfect beings, without the concourse of the male. With most of the lower animals and even with mammals, the ova show a trace of parthenogenetic power, for without being fertilised they pass through the first stages of segmentation.[8] Nor can pseudova which do not need fertilisation, be dis-

[5] Paget, 'Lectures on Pathology,' 1853, p. 158.

[6] Ibid., pp. 152, 164.

[7] Translated in 'Annals and Mag. of Nat. Hist.,' April, 1870, p. 272.

[8] Bischoff, as quoted by von Siebold, "Ueber Parthenogenesis," 'Sitzung der math. phys. Classe.' Munich, Nov. 4th, 1871, p. 240. *See* also Quatrefages, 'Annales des Sc. Nat. Zoolog., 3rd Series, 1850, p. 138.

tinguished from true ova, as was first shown by Sir J. Lubbock, and is now admitted by Siebold. So, again, the germ-balls in the larvæ of Cecidomyia are said by Leuckart [9] to be formed within the ovarium, but they do not require to be fertilised. It should also be observed that in sexual generation, the ovules and the male element have equal power of transmitting every single character possessed by either parent to their offspring. We see this clearly when hybrids are paired *inter se*, for the characters of both grandparents often appear in the progeny, either perfectly or by segments. It is an error to suppose that the male transmits certain characters and the female other characters; although no doubt, from unknown causes, one sex sometimes has a much stronger power of transmission than the other.

It has, however, been maintained by some authors that a bud differs essentially from a fertilised germ, in always reproducing the perfect character of the parent-stock; whilst fertilised germs give birth to variable beings. But there is no such broad distinction as this. In the eleventh chapter numerous cases were advanced showing that buds occasionally grow into plants having quite new characters; and the varieties thus produced can be propagated for a length of time by buds, and occasionally by seed. Nevertheless, it must be admitted that beings produced sexually are much more liable to vary than those produced asexually; and of this fact a partial explanation will hereafter be attempted. The variability in both cases is determined by the same general causes, and is governed by the same laws. Hence new varieties arising from buds cannot be distinguished from those arising from seed. Although bud-varieties usually retain their character during successive bud-generations, yet they occasionally revert, even after a long series of bud-generations, to their former character. This tendency to reversion in buds, is one of the most remarkable of the several points of agreement between the offspring from bud and seminal reproduction.

But there is one difference between organisms produced

[9] 'On the Asexual Reproduction of Cecidomyide Larvæ,' translated in 'Annals and Mag. of Nat. Hist., March, 1866, pp. 167, 171.

sexually and asexually, which is very general. The former pass in the course of their development from a very low stage to their highest stage, as we see in the metamorphoses of insects and of many other animals, and in the concealed metamorphoses of the vertebrata. Animals propagated asexually by buds or fission, on the other hand, commence their development at that stage at which the budding or self-dividing animal may happen to be, and therefore do not pass through some of the lower developmental stages.[10] Afterwards, they often advance in organisation, as we see in the many cases of "alternate generation." In thus speaking of alternate generation, I follow those naturalists who look at this process as essentially one of internal budding or of fissiparous generation. Some of the lower plants, however, such as mosses and certain algæ, according to Dr. L. Radlkofer,[11] when propagated asexually, do undergo a retrogressive metamorphosis. As far as the final cause is concerned, we can to a certain extent understand why beings propagated by buds should not pass through all the early stages of development; for with each organism the structure acquired at each stage must be adapted to its peculiar habits; and if there are places for the support of many individuals at some one stage, the simplest plan will be that they should be multiplied at this stage, and not that they should first retrograde in their development to an earlier or simpler structure, which might not be fitted for the then surrounding conditions.

From the several foregoing considerations we may conclude that the difference between sexual and asexual generation is not nearly so great as at first appears; the chief difference being that an ovule cannot continue to live and to be fully developed unless it unites with the male element; but even this difference is far from invariable, as shown by the many cases of parthenogenesis. We are therefore naturally led to inquire what the final cause can be of the necessity in

[10] Prof. Allman speaks ('Transact. R. Soc. of Edinburgh,' vol. xxvi., 1870, p. 102) decisively on this head with respect to the Hydroida: he says, "It "is a universal law in the succession "of zooids, that no retrogression ever "takes place in the series."

[11] 'Annals and Mag. of Nat. Hist., 2nd series, vol. xx., 1857, pp. 153–455

ordinary generation for the concourse of the two sexual elements.

Seeds and ova are often highly serviceable as the means o disseminating plants and animals, and of preserving them during one or more seasons in a dormant state; but unimpregnated seeds or ova, and detached buds, would be equally serviceable for both purposes. We can, however, indicate two important advantages gained by the concourse of the two sexes, or rather of two individuals belonging to opposite sexes; for, as I have shown in a former chapter, the structure of every organism appears to be especially adapted for the concurrence, at least occasionally, of two individuals. When species are rendered highly variable by changed conditions of life, the free intercrossing of the varying individuals tends to keep each form fitted for its proper place in nature; and crossing can be effected only by sexual generation; but whether the end thus gained is of sufficient importance to account for the first origin of sexual intercourse is extremely doubtful. Secondly, I have shown from a large body of facts, that, as a slight change in the conditions of life is beneficial to each creature, so, in an analogous manner, is the change effected in the germ by sexual union with a distinct individual; and I have been led, from observing the many widely-extended provisions throughout nature for this purpose, and from the greater vigour of crossed organisms of all kinds, as proved by direct experiments, as well as from the evil effects of close interbreeding when long continued, to believe that the advantage thus gained is very great.

Why the germ, which before impregnation undergoes a certain amount of development, ceases to progress and perishes, unless it be acted on by the male element; and why conversely the male element, which in the case of some insects is enabled to keep alive for four or five years, and in the case of some plants for several years, likewise perishes, unless it acts on or unites with the germ, are questions which cannot be answered with certainty. It is, however, probable that both sexual elements perish, unless brought into union, simply from including too little formative matter for independent development. Quatrefages has shown in the case of the Teredo,[12] as did formerly Prevost and Dumas with other animals, that more than one spermatozoon is requisite to fertilise an ovum. This has likewise been shown by Newport,[13] who proved by numerous experiments, that, when a very small number of spermatozoa are applied to the ova of Batrachians, they are only partially impregnated, and an embryo is never fully developed. The rate also of the segmentation of the ovum is determined by the number of the spermatozoa. With respect to plants, nearly the same results were obtained by Kölreuter and Gärtner. This last careful observer, after making successive trials on a Malva with more and more pollen-grains, found,[14] that even thirty grains did not fertilise a single seed; but when forty grains were applied to the stigma, a few seeds of small size were formed. In the case of Mirabilis the pollen grains are extraordinarily large, and the ovarium contains only a single ovule; and these circumstances led Naudin[15] to make the following experiments: a flower was fertilised by three grains and succeeded perfectly; twelve flowers were fertilised by two grains, and seventeen flowers by a single grain, and of these one flower alone in each lot perfected its seed: and it deserves especial notice that the plants produced by these two seeds never attained their proper dimensions, and bore flowers of remarkably small size. From these facts we clearly see that the quantity of the peculiar formative matter which is contained within the spermatozoa and pollen-grains is an all-important element in the act of fertilisation, not only for the full development of the seed, but for the vigour of the plant produced from such seed. We see something of the same kind in certain cases of parthenogenesis, that is, when the male element is wholly excluded; for M. Jourdan[16]

[12] 'Annales des Sc. Nat.,' 3rd series, 1850, tom. xiii.

[13] 'Transact. Phil. Soc.,' 1851, pp. 196, 208, 210; 1853, pp. 245, 247.

[14] 'Beitrage zur Kenntniss,' &c., 1844, s. 345.

[15] 'Nouvelles Archives du Muséum,' tom. i. p. 27.

[16] As quoted by Sir J. Lubbock in 'Nat. Hist. Review' 1862, p. 345. Weijenbergh also raised ('Nature,' Dec. 21, 1871, p. 149) two successive generations from unimpregnated females of another lepidopterous insect, *Liparis dispar*. These females did not produce at most one-twentieth of their full complement of eggs, and many of the eggs were worthless. Moreover the caterpillars raised from these unfertilised eggs "possessed far

found that, out of about 58,000 eggs laid by unimpregnated silk-moths, many passed through their early embryonic stages, showing that they were capable of self-development, but only twenty-nine out of the whole number produced caterpillars. The same principle of quantity seems to hold good even in artificial fissiparous reproduction, for Haeckel[17] found that by cutting the segmented and fertilised ova or larvæ of Siphonophoræ (jelly-fishes) into pieces, the smaller the pieces were, the slower was the rate of development, and the larvæ thus produced were by so much the more imperfect and inclined to monstrosity. It seems, therefore, probable that with the separate sexual elements deficient quantity of formative matter is the main cause of their not having the capacity for prolonged existence and development, unless they combine and thus increase each other's bulk. The belief that it is the function of the spermatozoa to communicate life to the ovule seems a strange one, seeing that the unimpregnated ovule is already alive and generally undergoes a certain amount of independent development. Sexual and asexual reproduction are thus seen not to differ essentially; and we have already shown that asexual reproduction, the power of re-growth and development are all parts of one and the same great law.

Re-growth of amputated parts.—This subject deserves a little further discussion. A multitude of the lower animals and some vertebrates possess this wonderful power. For instance, Spallanzani cut off the legs and tail of the same salamander six times successively, and Bonnet,[18] did so eight times; and on each occasion the limbs were reproduced on the exact line of amputation, with no part deficient or in excess. An allied animal, the axolotl, had a limb bitten off, which was reproduced in an abnormal condition, but when this was

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less vitality" than those from fertilised eggs. In the third parthenogenetic generation not a single egg yielded a caterpillar.

[17] 'Entwickelungsgeschichte der Siphonophora,' 1869, p. 73.

[18] Spallanzani, 'An Essay on Animal Reproduction,' translated by Dr. Maty, 1769, p. 79. Bonnet, 'Œuvres d'Hist. Nat.,' tom. v., part i., 4to. edit., 1781, pp. 343, 350.

amputated it was replaced by a perfect limb.[19] The new limbs in these cases bud forth, and are developed in the same manner as during the regular development of a young animal. For instance, with the *Amblystoma lurida*, three toes are first developed, then the fourth, and on the hind-feet the fifth, and so it is with a reproduced limb.[20]

The power of re-growth is generally much greater during the youth of an animal or during the earlier stages of its development than during maturity. The larvæ or tadpoles of the Batrachians are capable of reproducing lost members, but not so the adults.[21] Mature insects have no power of re-growth, excepting in one order, whilst the larvæ of many kinds have this power. Animals low in the scale are able, as a general rule, to reproduce lost parts far more easily than those which are more highly organised. The myriapods offer a good illustration of this rule; but there are some strange exceptions to it—thus Nemerteans, though lowly organised, are said to exhibit little power of re-growth. With the higher vertebrata, such as birds and mammals, the power is extremely limited.[22]

In the case of those animals which may be bisected or chopped into pieces, and of which every fragment will reproduce the whole, the power of re-growth must be diffused throughout the whole body. Nevertheless there seems to be much truth in the view maintained by Prof. Lessona,[23] that this capacity is generally a localised and special one, serving to replace parts which are eminently liable to be lost in each particular animal. The most striking case in favour of this view, is that the terrestrial salamander, according to Lessona, cannot reproduce lost parts, whilst another species of the

[19] Vulpian, as quoted by Prof. Faivre, 'La Variabilité des Espèces,' 1868, p. 112.

[20] Dr. P. Hoy, 'The American Naturalist,' Sept. 1871, p. 579.

[21] Dr. Günther, in Owen's 'Anatomy of Vertebrates,' vol. i., 1866, p. 567. Spallanzani has made similar observations.

[22] A thrush was exhibited before the British Association at Hull, in 1853, which had lost its tarsus, and this member, it was asserted, had been thrice reproduced; having been lost, I presume, each time by disease. Sir J. Paget informs me that he feels some doubt about the facts recorded by Sir J. Simpson ('Monthly Journal of Medical Science,' Edinburgh, 1848, new series, vol. ii. p. 890) of the re-growth of limbs in the womb in the case of man.

[23] 'Atti della Soc. Ital. di Sc. Nat.,' vol. xi., 1869, p. 493.

same genus, the aquatic salamander, has extraordinary powers of re-growth, as we have just seen; and this animal is eminently liable to have its limbs, tail, eyes and jaws bitten off by other tritons.[24] Even with the aquatic salamander the capacity is to a certain extent localised, for when M. Philipeaux,[25] extirpated the entire fore-limb together with the scapula, the power of re-growth was completely lost. It is also a remarkable fact, standing in opposition to a very general rule, that the young of the aquatic salamander do not possess the power of repairing their limbs in an equal degree with the adults;[26] but I do not know that they are more active, or can otherwise better escape the loss of their limbs, than the adults. The walking-stick insect, *Diapheromera femorata*, like other insects of the same order, can reproduce its legs in the mature state, and these from their great length must be liable to be lost: but the capacity is localised (as in the case of the salamander), for Dr. Scudder found,[27] that if the limb was removed within the trochanto-femoral articulation, it was never renewed. When a crab is seized by one of its legs, this is thrown off at the basal joint, being afterwards replaced by a new leg; and it is generally admitted that this is a special provision for the safety of the animal. Lastly, with gasteropod molluscs, which are well known to have the power of reproducing their heads, Lessona shows that they are very liable to have their heads bitten off by fishes; the rest of the body being protected by the shell. Even with plants we see something of the same kind, for non-deciduous leaves and young stems have no power of re-growth, these parts being easily replaced by growth from new buds; whilst the bark and subjacent tissues of the trunks of trees have great power of re-growth, probably on account of their increase in diameter, and of their liability to injury from being gnawed by animals.

[24] Lessona states that this is so in the paper just referred to. *See* also 'The American Naturalist,' Sept. 1871, p. 579.

[25] 'Comptes Rendus,' Oct. 1, 1866, and June, 1867.

[26] Bonnet, 'Œuvres Hist. Nat.,' vol. v. p. 294, as quoted by Prof. Rolleston in his remarkable address to the 36th annual meeting of the British Medical Association.

[27] 'Proc. Boston Soc. of Nat. Hist.,' vol. xii., 1868–69, p. 1.

Graft-hybrids.—It is well known from innumerable trials made in all parts of the world, that buds may be inserted into a stock, and that the plants thus raised are not affected in a greater degree than can be accounted for by changed nutrition. Nor do the seedlings raised from such inserted buds partake of the character of the stock, though they are more liable to vary than are seedlings from the same variety growing on its own roots. A bud, also, may sport into a new and strongly-marked variety without any other bud on the same plant being in the least degree affected. We may therefore infer, in accordance with the common view, that each bud is a distinct individual, and that its formative elements do not spread beyond the parts subsequently developed from it. Nevertheless, we have seen in the abstract on graft-hybridisation in the eleventh chapter that buds certainly include formative matter, which can occasionally combine with that included in the tissues of a distinct variety or species; a plant intermediate between the two parent-forms being thus produced. In the case of the potato we have seen that the tubers produced from a bud of one kind inserted into another are intermediate in colour, size, shape and state of surface; that the stems, foliage, and even certain constitutional peculiarities, such as precocity, are likewise intermediate. With these well-established cases, the evidence that graft-hybrids have also been produced with the laburnum, orange, vine, rose, &c., seems sufficient. But we do not know under what conditions this rare form of reproduction is possible. From these several cases we learn the important fact that formative elements capable of blending with those of a distinct individual (and this is the chief characteristic of sexual generation), are not confined to the reproductive organs, but are present in the buds and cellular tissue of plants; and this is a fact of the highest physiological importance.

Direct Action of the Male Element on the Female.—In the eleventh chapter, abundant proofs were given that foreign pollen occasionally affects in a direct manner the mother-plant. Thus, when Gallesio fertilised an orange-flower with pollen from the lemon, the fruit bore stripes of perfectly characterised lemon-peel. With peas, several observers have seen the colour of the seed-coats and even of the pod directly affected by the pollen of a distinct variety. So it has been with the fruit of the apple, which consists of the modified calyx and upper part of the flower-stalk. In ordinary cases these parts are wholly formed by the mother-plant. We here see that the formative elements included within the male element or pollen of one variety can affect and hybridise, not the part which they are properly adapted to affect, namely, the ovules, but the partially-developed tissues of a distinct variety or species. We are thus brought half-way towards a graft-hybrid, in which the formative elements included within the tissues of one individual combine with those included in the tissues of a distinct variety or species, thus giving rise to a new and intermediate form, independently of the male or female sexual organs.

With animals which do not breed until nearly mature, and of which all the parts are then fully developed, it is hardly possible that the male element should directly affect the female. But we have the analogous and perfectly well-ascertained case of the male element affecting (as with the quagga and Lord Morton's mare) the female or her ova, in such a manner that when she is impregnated by another male her offspring are affected and hybridised by the first male. The explanation would be simple if the spermatozoa could keep alive within the body of the female during the long interval which has sometimes elapsed between the two acts of impregnation; but no one will suppose that this is possible with the higher animals.

Development.—The fertilised germ reaches maturity by a vast number of changes: these are either slight and slowly effected, as when the child grows into the man, or are great and sudden, as with the metamorphoses of most insects. Between these extremes we have every gradation, even within the same class; thus, as Sir J. Lubbock has shown,[28] there is an Ephemerous insect which moults above twenty times, undergoing each time a slight but decided change of structure; and these changes, as he further remarks, probably reveal to

[28] 'Transact. Linn. Soc.,' vol. xxiv., 1863, p. 62.

us the normal stages of development, which are concealed and hurried through or suppressed in most other insects. In ordinary metamorphoses, the parts and organs appear to become changed into the corresponding parts in the next stage of development; but there is another form of development, which has been called by Professor Owen metagenesis. In this case "the new parts are not moulded upon the inner "surface of the old ones. The plastic force has changed its "course of operation. The outer case, and all that gave form "and character to the precedent individual, perish and are "cast off; they are not changed into the corresponding parts "of the new individual. These are due to a new and distinct "developmental process," &c.[29] Metamorphosis, however, graduates so insensibly into metagenesis, that the two processes cannot be distinctly separated. For instance, in the last change which Cirripedes undergo, the alimentary canal and some other organs are moulded on pre-existing parts; but the eyes of the old and the young animal are developed in entirely different parts of the body; the tips of the mature limbs are formed within the larval limbs, and may be said to be metamorphosed from them; but their basal portions and the whole thorax are developed in a plane at right angles to the larval limbs and thorax; and this may be called metagenesis. The metagenetic process is carried to an extreme point in the development of some Echinoderms, for the animal in the second stage of development is formed almost like a bud within the animal of the first stage, the latter being then cast off like an old vestment, yet sometimes *maintaining for a short period an independent* vitality.[30]

If, instead of a single individual, several were to be thus developed metagenetically within a pre-existing form, the process would be called one of alternate generation. The young thus developed may either closely resemble the encasing

[29] 'Parthenogenesis,' 1849, pp. 25, 26. Prof. Huxley has some excellent remarks ('Medical Times,' 1856, p. 637) on this subject in reference to the development of star-fishes, and shows how curiously metamorphosis graduates into gemmation or zoid-formation, which is in fact the same as metagenesis.

[30] Prof. J. Reay Greene, in Günther's 'Record of Zoolog. Lit.,' 1865, p. 625.

parent-form, as with the larvæ of Cecidomyia, or may differ to an astonishing degree, as with many parasitic worms and jelly-fishes; but this does not make any essential difference in the process, any more than the greatness or abruptness of the change in the metamorphoses of insects.

The whole question of development is of great importance for our present subject. When an organ, the eye, for instance, is metagenetically formed in a part of the body where during the previous stage of development no eye existed, we must look at it as a new and independent growth. The absolute independence of new and old structures, although corresponding in structure and function, is still more obvious when several individuals are formed within a previous form, as in the cases of alternate generation. The same important principle probably comes largely into play even in the case of apparently continuous growth, as we shall see when we consider the inheritance of modifications at corresponding ages.

We are led to the same conclusion, namely, the independence of parts successively developed, by another and quite distinct group of facts. It is well known that many animals belonging to the same order, and therefore not differing widely from each other, pass through an extremely different course of development. Thus certain beetles, not in any way remarkably different from others of the same order, undergo what has been called a hyper-metamorphosis—that is, they pass through an early stage wholly different from the ordinary grub-like larva. In the same sub-order of crabs, namely, the Macroura, as Fritz Müller remarks, the river cray-fish is hatched under the same form which it ever afterwards retains; the young lobster has divided legs, like a Mysis; the Palæmon appears under the form of a Zoea, and Peneus under the Nauplius-form; and how wonderfully these larval forms differ from one another, is known to every naturalist.[31] Some other crustaceans, as the same author observes, start from the same point and arrive at nearly the same end, but in the

[31] Fritz Müller's 'Für Darwin,' 1864, s. 65, 71. The highest authority on crustaceans, Prof. Milne-Edwards, insists ('Annal. des Sci. Nat.,' 2nd series, Zoolog., tom. iii. p. 322) on the difference in the metamorphosis of closely-allied genera.

middle of their development are widely different from one another. Still more striking cases could be given with respect to the Echinodermata. With the Medusæ or jelly-fishes Professor Allman observes, "The classification of the "Hydroida would be a comparatively simple task if, as has "been erroneously asserted, generically-identical medusoids "always arose from generically-identical polypoids; and, on "the other hand, that generically-identical polypoids always "gave origin to generically-identical medusoids." So again, Dr. Strethill Wright remarks, "In the life-history of the "Hydroidæ any phase, planuloid, polypoid, or medusoid, may "be absent."[32]

According to the belief now generally accepted by our best naturalists, all the members of the same order or class, for instance, the Medusæ or the Macrourous crustaceans, are descended from a common progenitor. During their descent they have diverged much in structure, but have retained much in common; and this has occurred, though they have passed through and still pass through marvellously different metamorphoses. This fact well illustrates how independent each structure is from that which precedes and that which follows it in the course of development.

The Functional Independence of the Elements or Units of the Body.—Physiologists agree that the whole organism consists of a multitude of elemental parts, which are to a great extent independent of one another. Each organ, says Claude Bernard,[33] has its proper life, its autonomy; it can develop and reproduce itself independently of the adjoining tissues. A great German authority, Virchow,[34] asserts still more emphatically that each system consists of an "enormous "mass of minute centres of action. . . . . Every element has "its own special action, and even though it derive its stimulus "to activity from other parts, yet alone effects the actual "performance of duties. . . . . Every single epithelial and

[32] Prof. Allman, in 'Annals and Mag. of Nat. Hist.,' 3rd series, vol. xiii., 1864, p. 348; Dr. S. Wright, ibid., vol. viii., 1861, p. 127. *See* also p. 358 for analogous statements by Sars.

[33] 'Tissus Vivants,' 1866, p. 22.

[34] '*Cellular Pathology*,' *translat.* by Dr. Chance, 1860, pp. 14, 18, 83, 460.

"muscular fibre-cell leads a sort of parasitical existence in "relation to the rest of the body. . . . . Every single bone-"corpuscle really possesses conditions of nutrition peculiar to "itself." Each element, as Sir J. Paget remarks, lives its appointed time and then dies, and is replaced after being cast off or absorbed.[35] I presume that no physiologist doubts that, for instance, each bone-corpuscle of the finger differs from the corresponding corpuscle in the corresponding joint of the toe; and there can hardly be a doubt that even those on the corresponding sides of the body differ, though almost identical in nature. This near approach to identity is curiously shown in many diseases in which the same exact points on the right and left sides of the body are similarly affected; thus Sir J. Paget[36] gives a drawing of a diseased pelvis, in which the bone has grown into a most complicated pattern, but "there is not one spot or line on one side which "is not represented, as exactly as it would be in a mirror, on "the other."

Many facts support this view of the independent life of each minute element of the body. Virchow insists that a single bone-corpuscle or a single cell in the skin may become diseased. The spur of a cock, after being inserted into the ear of an ox, lived for eight years, and acquired a weight of 396 grammes (nearly fourteen ounces), and the astonishing length of twenty-four centimetres, or about nine inches; so that the head of the ox appeared to bear three horns.[37] The tail of a pig has been grafted into the middle of its back, and reacquired sensibility. Dr. Ollier[38] inserted a piece of periosteum from the bone of a young dog under the skin of a rabbit, and true bone was developed. A multitude of similar facts could be given. The frequent presence of hairs and of perfectly developed teeth, even teeth of the second dentition, in ovarian tumours,[39] are facts leading to the same conclusion.

[35] Paget, 'Surgical Pathology,' vol. i., 1853, pp. 12–14.

[36] Ibid., p. 19.

[37] *See* Prof. Mantegazza's interesting work, 'Degli innesti Animali,' &c., Milano, 1865, p. 51, tab. 3.

[38] 'De la Production Artificielle des Os,' p. 8.

[39] Isidore Geoffroy Saint-Hilaire, 'Hist. des Anomalies,' tom. ii. pp. 549, 560, 562; Virchow, ibid., p. 484. Lawson Tait, 'The Pathology of Diseases of the Ovaries,' 1874, pp. 61, 62.

Mr. Lawson Tait refers to a tumour in which "over 300 *teeth were found, resembling in many respects milk-teeth;*" and to another tumour, "full of hair which had grown and "been shed from one little spot of skin not bigger than the tip "of my little finger. The amount of hair in the sac, had it "grown from a similarly sized area of the scalp, would have "taken almost a lifetime to grow and be shed."

Whether each of the innumerable autonomous elements of the body is a cell or the modified product of a cell, is a more doubtful question, even if so wide a definition be given to the term, as to include cell-like bodies without walls and without nuclei.[40] The doctrine of *omnis cellula e cellulâ* is admitted for plants, and widely prevails with respect to animals.[41] Thus Virchow, the great supporter of the cellular theory, whilst allowing that difficulties exist, maintains that every atom of tissue is derived from cells, and these from pre-existing cells, and these primarily from the egg, which he regards as a great cell. That cells, still retaining the same nature, increase by self-division or proliferation, is admitted by every one. But when an organism undergoes great changes of structure during development, the cells, which at each stage are supposed to be directly derived from previously existing cells, must likewise be greatly changed in nature; this change is attributed by the supporters of the cellular doctrine to some inherent power which the cells possess, and not to any external agency. Others maintain that cells and tissues of all kinds may be formed, independently of pre-existing cells, from plastic lymph or blastema. Whichever view may be correct, every one admits that the body consists of a multitude of organic units, all of which possess their own proper attributes, and are to a certain extent independent of all others. Hence it will be convenient to use indifferently the terms cells or organic units, or simply units.

Variability and Inheritance.—We have seen in the twenty-second chapter that variability is not a principle co-ordinate with life or reproduction, but results from special causes,

[40] For the most recent classification of cells, *see* Ernst Häckel's 'Generelle Morpholog.,' Band ii., 1866, s. 275.

[41] Dr. W. Turner, 'The Present Aspect of Cellular Pathology,' 'Edinburgh Medical Journal,' April, 1863.

generally from changed conditions acting during successive generations. The fluctuating variability thus induced is apparently due in part to the sexual system being easily affected, so that it is often rendered impotent; and when not so seriously affected, it often fails in its proper function of transmitting truly the characters of the parents to the offspring. But variability is not necessarily connected with the sexual system, as we see in the cases of bud-variation. Although we are seldom able to trace the nature of the connection, many deviations of structure no doubt result from changed conditions acting directly on the organisation, independently of the reproductive system. In some instances we may feel sure of this, when all, or nearly all the individuals which have been similarly exposed are similarly and definitely affected, of which several instances have been given. But it is by no means clear why the offspring should be affected by the exposure of the parents to new conditions, and why it is necessary in most cases that several generations should have been thus exposed.

How, again, can we explain the inherited effects of the use or disuse of particular organs? The domesticated duck flies less and walks more than the wild duck, and its limb-bones have become diminished and increased in a corresponding manner in comparison with those of the wild duck. A horse is trained to certain paces, and the colt inherits similar consensual movements. The domesticated rabbit becomes tame from close confinement; the dog, intelligent from associating with man; the retriever is taught to fetch and carry; and these mental endowments and bodily powers are all inherited. Nothing in the whole circuit of physiology is more wonderful. How can the use or disuse of a particular limb or of the brain affect a small aggregate of reproductive cells, seated in a distant part of the body, in such a manner that the being developed from these cells inherits the characters of either one or both parents? Even an imperfect answer to this question would be satisfactory.

In the chapters devoted to inheritance it was shown that a multitude of newly-acquired characters, whether injurious or beneficial, whether of the lowest or highest vital importance, are often faithfully transmitted—frequently even when one parent alone possesses some new peculiarity; and we may on the whole conclude that inheritance is the rule, and non-inheritance the anomaly. In some instances a character is not inherited, from the conditions of life being directly opposed to its development; in many instances, from the conditions incessantly inducing fresh variability, as with grafted fruit-trees and highly-cultivated flowers. In the remaining cases the failure may be attributed to reversion, by which the child resembles its grandparents or more remote progenitors, instead of its parents.

Inheritance is governed by various laws. Characters which first appear at any particular age tend to reappear at a corresponding age. They often become associated with certain seasons of the year, and reappear in the offspring at a corresponding season. If they appear rather late in life in one sex, they tend to reappear exclusively in the same sex at the same period of life.

The principle of reversion, recently alluded to, is one of the most wonderful of the attributes of Inheritance. It proves to us that the transmission of a character and its development, which ordinarily go together and thus escape discrimination, are distinct powers; and these powers in some cases are even antagonistic, for each acts alternately in successive generations. Reversion is not a rare event, depending on some unusual or favourable combination of circumstances, but occurs so regularly with crossed animals and plants, and so frequently with uncrossed breeds, that it is evidently an essential part of the principle of inheritance. We know that changed conditions have the power of evoking long-lost characters, as in the case of animals becoming feral. The act of crossing in itself possesses this power in a high degree. What can be more wonderful than that characters, which have disappeared during scores, or hundreds, or even thousands of generations, should suddenly reappear perfectly developed, as in the case of pigeons and fowls, both when purely bred and especially when crossed; or as with the zebrine stripes on dun-coloured horses, and other such cases? Many monstrosities come under this same head, as when rudimentary organs are redeveloped, or when an organ which we must believe was possessed by an early progenitor of the species, but of which not even a rudiment is left, suddenly reappears, as with the fifth stamen in some Scrophulariaceæ. We have already seen that reversion acts in bud-reproduction; and we know that it occasionally acts during the growth of the same individual animal, especially, but not exclusively, if of crossed parentage,—as in the rare cases described of fowls, pigeons, cattle, and rabbits, which have reverted to the colours of one of their parents or ancestors as they advanced in years.

We are led to believe, as formerly explained, that every character which occasionally reappears is present in a latent form in each generation, in nearly the same manner as in male and female animals the secondary characters of the opposite sex lie latent and ready to be evolved when the reproductive organs are injured. This comparison of the secondary sexual characters which lie latent in both sexes, with other latent characters, is the more appropriate from the case recorded of a Hen, which assumed some of the masculine characters, not of her own race, but of an early progenitor; she thus exhibited at the same time the re-development of latent characters of both kinds. In every living creature we may feel assured that a host of long-lost characters lie ready to be evolved under proper conditions. How can we make intelligible and connect with other facts, this wonderful and common capacity of reversion,—this power of calling back to life long-lost characters?

PART II.

I have now enumerated the chief facts which every one would desire to see connected by some intelligible bond. This can be done, if we make the following assumptions, and much may be advanced in favour of the chief one. The secondary assumptions can likewise be supported by various physiological considerations. It is universally admitted that the cells or units of the body increase by self-division or proliferation, retaining the same nature, and that they ultimately become converted into the various tissues and substances of the body. But besides this means of increase I assume that the units throw off minute granules which are dispersed throughout the whole system; that these, when supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived. These granules may be called gemmules. They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being; but they are likewise capable of transmission in a dormant state to future generations and may then be developed. Their development depends on their union with other partially developed or nascent cells which precede them in the regular course of growth. Why I use the term union, will be seen when we discuss the direct action of pollen on the tissues of the mother-plant. Gemmules are supposed to be thrown off by every unit, not only during the adult state, but during each stage of development of every organism; but not necessarily during the continued existence of the same unit. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation into buds or into the sexual elements. Hence, it is not the reproductive organs or buds which generate new organisms, but the units of which each individual is composed. These assumptions constitute the provisional hypothesis which I have called Pangenesis. Views in many respects similar have been propounded by various authors.[42]

[42] Mr. G. H. Lewes ('Fortnightly Review,' Nov. 1, 1868, p. 506) remarks on the number of writers who have advanced nearly similar views. More than two thousand years ago Aristotle combated a view of this kind, which, as I hear from Dr. W. Ogle, was held by Hippocrates and others. Ray, in his 'Wisdom of God' (2nd edit., 1692, p. 68), says that "every part "of the body seems to club and con- "tribute to the seed." The "organic molecules" of Buffon ('Hist. Nat. Gen.,' edit. of 1749, tom. ii. pp. 54, 62, 329, 333, 420, 425) appear at first sight to be the same as the gemmules of my hypothesis, but they are essentially different. Bonnet ('Œuvres d'Hist. Nat.,' tom. v., part i., 1781, 4to edit., p. 334) speaks of the limbs having germs adapted for the reparation of all possible losses; but whether these germs are supposed to be the same with those within buds and the sexual organs is not clear. Prof. Owen says ('Anatomy of Vertebrates,' vol. iii., 1868, p. 813) that he fails to see any fundamental difference between the views which he propounded in his 'Parthenogenesis' (1849, pp. 5–8), and which he now considers as erroneous, and my hypothesis of pangenesis: but a reviewer ('Journal of Anat. and Phys.,' May, 1869,

Before proceeding to show, firstly, how far these assumptions are in themselves probable, and secondly, how far they connect and explain the various groups of facts with which we are concerned, it may be useful to give an illustration, as simple as possible, of the hypothesis. If one of the Protozoa be formed, as it appears under the microscope, of a small mass of homogeneous gelatinous matter, a minute particle or gemmule thrown off from any part and nourished under favourable circumstances would reproduce the whole; but if the upper and lower surfaces were to differ in texture from each other and from the central portion, then all three parts would have to throw off gemmules, which when aggregated by mutual affinity would form either buds or the sexual elements, and would ultimately be developed into a similar organism. Precisely the same view may be extended to one of the higher animals;, although in this case many thousand gemmules must be thrown off from the various parts of the body at each stage of development; these gemmules being developed in union with pre-existing nascent cells in due order of succession.

Physiologists maintain, as we have seen, that each unit of the body, though to a large extent dependent on others, is likewise to a certain extent independent or autonomous, and has the power of increasing by self-division. I go one step further, and assume that each unit casts off free gemmules which are dispersed throughout the system, and are capable under proper conditions of being developed into similar units. Nor can this assumption be considered as gratuitous and improbable. It is manifest that the sexual elements and buds include formative matter of some kind, capable of development; and we now know from the production of graft-hybrids that similar matter is dispersed throughout the tissues of

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p. 441) shows how different they really are. I formerly thought that the "physiological units" of Herbert Spencer ('Principles of Biology,' vol. i., chaps. iv. and viii., 1863–64) were the same as my gemmules, but I now know that this is not the case. Lastly, it appears from a review of the present work by Prof. Mantegazza ('Nuova Antologia, Maggio,' 1868), that he (in his 'Elementi di Igiene,' Ediz. iii., p. 540) clearly foresaw the doctrine of pangenesis.

plants, and can combine with that of another and distinct plant, giving rise to a new being, intermediate in character. We know also that the male element can act directly on the partially developed tissues of the mother-plant, and on the future progeny of female animals. The formative matter which is thus dispersed throughout the tissues of plants, and which is capable of being developed into each unit or part, must be generated there by some means; and my chief assumption is that this matter consists of minute particles or gemmules cast off from each unit or cell.[43]

But I have further to assume that the gemmules in their undeveloped state are capable of largely multiplying themselves by self-division, like independent organisms. Delpino insists that to "admit of multiplication by fissiparity in corpuscles, "analogous to seeds or buds . . . is repugnant to all analogy." But this seems a strange objection, as Thuret[44] has seen the zoospore of an alga divide itself, and each half germinated. Haeckel divided the segmented ovum of a siphonophora into many pieces, and these were developed. Nor does the extreme minuteness of the gemmules, which can hardly differ much in nature from the lowest and simplest organisms, render it improbable that they should grow and multiply. A great authority, Dr. Beale,[45] says "that minute yeast cells are "capable of throwing off buds or gemmules, much less than "the $\frac{1}{100000}$ of an inch in diameter;" and these he thinks are "capable of subdivision practically ad infinitum."

A particle of small-pox matter, so minute as to be borne by the wind, must multiply itself many thousandfold in a person thus inoculated; and so with the contagious matter of scarlet fever.[46] It has recently been ascertained[47] that a minute portion of the mucous discharge from an animal affected with

[43] Mr. Lowne has observed ('Journal of Queckett Microscopical Club,' Sept. 23, 1870) certain remarkable changes in the tissues of the larva of a fly, which makes him believe "it "possible that organs and organisms "are sometimes developed by the "aggregation of excessively minute "gemmules, such as those which Mr. "Darwin's hypothesis demands."

[44] 'Annales des Sc. Nat.,' 3rd series, Bot., tom. xiv., 1850, p. 244.

[45] 'Disease Germs,' p. 20.

[46] *See* some very interesting papers on this subject by Dr. Beale, in 'Medical Times and Gazette,' Sept. 9th, 1865, pp. 273, 330.

[47] Third Report of the R. Comm. on the Cattle Plague, as quoted in 'Gard. Chronicle,' 1866, p. 446.

rinderpest, if placed in the blood of a healthy ox, increases so fast that in a short space of time "the whole mass of "blood, weighing many pounds, is infected, and every small "particle of that blood contains enough poison to give, "within less than forty-eight hours, the disease to another "animal."

The retention of free and undeveloped gemmules in the same body from early youth to old age will appear improbable, but we should remember how long seeds lie dormant in the earth and buds in the bark of a tree. Their transmission from generation to generation will appear still more improbable; but here again we should remember that many rudimentary and useless organs have been transmitted during an indefinite number of generations. We shall presently see how well the long-continued transmission of undeveloped gemmules explains many facts.

As each unit, or group of similar units, throughout the body, casts off its gemmules, and as all are contained within the smallest ovule, and within each spermatozoon or pollen-grain, and as some animals and plants produce an astonishing number of pollen-grains and ovules,[48] the number and minuteness of the gemmules must be something inconceivable. But considering how minute the molecules are, and how many go to the formation of the smallest granule of any ordinary substance, this difficulty with respect to the gemmules is not insuperable. From the data arrived at by Sir W. Thomson, my son George finds that a cube of $\frac{1}{10000}$ of an inch of glass or water must consist of between 16 million millions, and 131 thousand million million molecules. No doubt the molecules of which an organism is formed are larger, from being more complex, than those of an inorganic substance, and probably

[48] Mr. F. Buckland found 6,867,840 eggs in a cod-fish ('Land and Water,' 1868, p. 62). An Ascaris produces about 64,000,000 eggs (Carpenter's 'Comp. Phys.,' 1854, p. 590). Mr. J. Scott, of the Royal Botanic Garden of Edinburgh, calculated, in the same manner as I have done for some British Orchids ('Fertilisation of Orchids,' p. 344), the number of seeds in a capsule of an Acropera and found the number to be 371,250. Now this plant produces several flowers on a raceme, and many racemes during a season. In an allied genus, Gongora, Mr. Scott has seen twenty capsules produced on a single raceme; ten such racemes on the Acropera would yield above seventy-four millions of seed.

many molecules go to the formation of a gemmule; but when we bear in mind that a cube of $\frac{1}{10000}$ of an inch is much smaller than any pollen-grain, ovule or bud, we can see what a vast number of gemmules one of these bodies might contain.

The gemmules derived from each part or organ must be thoroughly dispersed throughout the whole system. We know, for instance, that even a minute fragment of a leaf of a Begonia will reproduce the whole plant; and that if a fresh-water worm is chopped into small pieces, each will reproduce the whole animal. Considering also the minuteness of the gemmules and the permeability of all organic tissues, the thorough dispersion of the gemmules is not surprising. That matter may be readily transferred without the aid of vessels from part to part of the body, we have a good instance in a case recorded by Sir J. Paget of a lady, whose hair lost its colour at each successive attack of neuralgia and recovered it again in the course of a few days. With plants, however, and probably with compound animals, such as corals, the gemmules do not ordinarily spread from bud to bud, but are confined to the parts developed from each separate bud; and of this fact no explanation can be given.

The assumed elective affinity of each gemmule for that particular cell which precedes it in due order of development is supported by many analogies. In all ordinary cases of sexual reproduction, the male and female elements certainly have a mutual affinity for each other: thus, it is believed that about ten thousand species of Compositæ exist, and there can be no doubt that if the pollen of all these species could be simultaneously or successively placed on the stigma of any one species, this one would elect with unerring certainty its own pollen. This elective capacity is all the more wonderful, as it must have been acquired since the many species of this great group of plants branched off from a common progenitor. On any view of the nature of sexual reproduction, the formative matter of each part contained within the ovules and the male element act on each other by some law of special affinity, so that corresponding parts affect one another; thus, a calf produced from a short-horned cow by a long-horned bull has its horns affected by the union of the two forms, and the offspring from two birds with differently coloured tails have their tails affected.

The various tissues of the body plainly show, as many physiologists have insisted,[49] an affinity for special organic substances, whether natural or foreign to the body. We see this in the cells of the kidneys attracting urea from the blood; in curare affecting certain nerves; *Lytta vesicatoria* the kidneys; and the poisonous matter of various diseases, as small-pox, scarlet-fever, hooping-cough, glanders, and hydrophobia, affecting certain definite parts of the body.

It has also been assumed that the development of each gemmule depends on its union with another cell or unit which has just commenced its development, and which precedes it in due order of growth. That the formative matter within the pollen of plants, which by our hypothesis consists of gemmules, can unite with and modify the partially developed cells of the mother-plant, we have clearly seen in the section devoted to this subject. As the tissues of plants are formed, as far as is known, only by the proliferation of pre-existing cells, we must conclude that the gemmules derived from the foreign pollen do not become developed into new and separate cells, but penetrate and modify the nascent cells of the mother-plant. This process may be compared with what takes place in the act of ordinary fertilisation, during which the contents of the pollen-tubes penetrate the closed embryonic sac within the ovule, and determine the development of the embryo. According to this view, the cells of the mother-plant may almost literally be said to be fertilised by the gemmules derived from the foreign pollen. In this case and in all others the proper gemmules must combine in due order with pre-existing nascent cells, owing to their elective affinities. A slight difference in nature between the gemmules and the nascent cells would be far from interfering with their mutual union and development, for we well know in the case of ordinary reproduction that such slight differentia-

[49] Paget, 'Lectures on Pathology,' p. 27; Virchow, 'Cellular Pathology,' translat. by Dr. Chance, pp. 123, 126, 294. Claude Bernard, 'Des Tissus Vivants,' pp. 177, 210, 337; Müller's 'Physiology,' Eng. translat., p. 290.

tion in the sexual elements favours in a marked manner their union and subsequent development, as well as the vigour of the offspring thus produced.

Thus far we have been able by the aid of our hypothesis to throw some obscure light on the problems which have come before us; but it must be confessed that many points remain altogether doubtful. Thus it is useless to speculate at what period of development each unit of the body casts off its gemmules, as the whole subject of the development of the various tissues is as yet far from clear. We do not know whether the gemmules are merely collected by some unknown means at certain seasons within the reproductive organs, or whether after being thus collected they rapidly multiply there, as the flow of blood to these organs at each breeding season seems to render probable. Nor do we know why the gemmules collect to form buds in certain definite places, leading to the symmetrical growth of trees and corals. We have no means of deciding whether the ordinary wear and tear of the tissues is made good by means of gemmules, or merely by the proliferation of pre-existing cells. If the gemmules are thus consumed, as seems probable from the intimate connection between the repair of waste, regrowth, and development, and more especially from the periodical changes which many male animals undergo in colour and structure, then some light would be thrown on the phenomena of old age, with its lessened power of reproduction and of the repair of injuries, and on the obscure subject of longevity. The fact of castrated animals, which do not cast off innumerable gemmules in the act of reproduction, not being longer-lived than perfect males, seems opposed to the belief that gemmules are consumed in the ordinary repair of wasted tissues; unless indeed the gemmules after being collected in small numbers within the reproductive organs are there largely multiplied.[50]

That the same cells or units may live for a long period and

[50] Prof. Ray Lankester has discussed several of the points here referred to as bearing on pangenesis, in his interesting essay, 'On Comparative Longevity in Man and the Lower Animals,' 1870, pp. 33, 77, &c.

continue multiplying without being modified by their union with free gemmules of any kind, is probable from such cases as that of the spur of a cock which grew to an enormous size when grafted into the ear of an ox. How far units are modified during their normal growth by absorbing peculiar nutriment from the surrounding tissues, independently of their union with gemmules of a distinct nature, is another doubtful point.[51] We shall appreciate this difficulty by calling to mind what complex yet symmetrical growths the cells of plants yield when inoculated by the poison of a gall-insect. With animals various polypoid excrescences and tumours are generally admitted[52] to be the direct product, through proliferation, of normal cells which have become abnormal. In the regular growth and repair of bones, the tissues undergo, as Virchow remarks,[53] a whole series of permutations and substitutions. "The cartilage cells may "be converted by a direct transformation into marrow-cells, "and continue as such; or they may first be converted into "osseous and then into medullary tissue; or lastly, they may "first be converted into marrow and then into bone. So "variable are the permutations of these tissues, in themselves "so nearly allied, and yet in their external appearance so "completely distinct." But as these tissues thus change their nature at any age, without any obvious change in their nutrition, we must suppose in accordance with our hypothesis that gemmules derived from one kind of tissue combine with the cells of another kind, and cause the successive modifications.

We have good reason to believe that several gemmules are requisite for the development of one and the same unit or cell; for we cannot otherwise understand the insufficiency of a single or even of two or three pollen-grains or spermatozoa. But we are far from knowing whether the gemmules of all the units are free and separate from one another, or whether some are from the first united into small aggregates.

[51] Dr. Ross refers to this subject in his 'Graft Theory of Disease,' 1872, p. 53.

[52] Virchow, 'Cellular Pathology,' trans. by Dr. Chance, 1860, pp. 60, 162, 245, 441, 454.

[53] Ibid., pp. 412–426.

A feather, for instance, is a complex structure, and, as each separate part is liable to inherited variations, I conclude that each feather generates a large number of gemmules; but it is possible that these may be aggregated into a compound gemmule. The same remark applies to the petals of flowers, which are sometimes highly complex structures, with each ridge and hollow contrived for a special purpose, so that each part must have been separately modified, and the modifications transmitted; consequently, separate gemmules, according to our hypothesis, must have been thrown off from each cell or unit. But, as we sometimes see half an anther or a small portion of a filament becoming petali-form, or parts or mere stripes of the calyx assuming the colour and texture of the corolla, it is probable that with petals the gemmules of each cell are not aggregated together into a compound gemmule, but are free and separate. Even in so simple a case as that of a perfect cell, with its protoplasmic contents, nucleus, nucleolus, and walls, we do not know whether or not its development depends on a compound gemmule derived from each part.[54]

Having now endeavoured to show that the several foregoing assumptions are to a certain extent supported by analogous facts, and having alluded to some of the most doubtful points, we will consider how far the hypothesis brings under a single point of view the various cases enumerated in the First Part. All the forms of reproduction graduate into one another and agree in their product; for it is impossible to distinguish between organisms produced from buds, from self-division, or from fertilised germs; such organisms are liable to variations of the same nature and to reversions of the same kind; and as, according to our hypothesis, all the forms of reproduction depend on the aggregation of gemmules derived from the whole body, we can understand this remarkable agreement. Parthenogenesis is no longer wonderful, and if we did not know that great good followed from the union of the sexual elements derived from two distinct individuals, the

[54] See some good criticisms on this head by Delpino, and by Mr. G. H. Lewes in the 'Fortnightly Review,' Nov. 1, 1868, p. 509.

wonder would be that parthenogenesis did not occur much oftener than it does. On any ordinary theory of reproduction the formation of graft-hybrids, and the action of the male element on the tissues of the mother-plant, as well as on the future progeny of female animals, are great anomalies; but they are intelligible on our hypothesis. The reproductive organs do not actually create the sexual elements; they merely determine the aggregation and perhaps the multiplication of the gemmules in a special manner. These organs, however, together with their accessory parts, have high functions to perform. They adapt one or both elements for independent temporary existence, and for mutual union. The stigmatic secretion acts on the pollen of a plant of the same species in a wholly different manner to what it does on the pollen of one belonging to a distinct genus or family. The spermatophores of the Cephalopoda are wonderfully complex structures, which were formerly mistaken for parasitic worms; and the spermatozoa of some animals possess attributes which, if observed in an independent animal, would be put down to instinct guided by sense-organs,—as when the spermatozoa of an insect find their way into the minute micropyle of the egg.

The antagonism which has long been observed,[55] with certain exceptions, between growth and the power of sexual reproduction [56]—between the repair of injuries and gemmation—and with plants, between rapid increase by buds, rhizomes, &c., and the production of seed, is partly explained by the gemmules not existing in sufficient numbers for these processes to be carried on simultaneously.

[55] Mr. Herbert Spencer ('Principles of Biology,' vol. ii. p. 430) has fully discussed this antagonism.

[56] The male salmon is known to breed at a very early age. The Triton and Siredon, whilst retaining their larval branchiæ, according to Filippi and Duméril ('Annals and Mag. of Nat. Hist.,' 3rd series, 1866, p. 157), are capable of reproduction. Ernst Haeckel has recently ('Monatsbericht Akad. Wiss. Berlin,' Feb. 2nd, 1865) observed the surprising case of a medusa, with its reproductive organs active, which produces by budding a widely different form of medusa; and this latter also has the power of sexual reproduction. Krohn has shown ('Annals and Mag. of Nat. Hist.,' 3rd series, vol. xix., 1862, p. 6) that certain other medusæ, whilst sexually mature, propagate by gemmæ. *See*, also, Kolliker, 'Morphologie und Entwickelungsgeschichte des Pennatulidenstammes,' 1872, p. 12.

Hardly any fact in physiology is more wonderful than the power of re-growth; for instance, that a snail should be able to reproduce its head, or a salamander its eyes, tail, and legs, exactly at the points where they have been cut off. Such cases are explained by the presence of gemmules derived from each part, and disseminated throughout the body. I have heard the process compared with that of the repair of the broken angles of a crystal by re-crystallisation; and the two processes have this much in common, that in the one case the polarity of the molecules is the efficient cause, and in the other the affinity of the gemmules for particular nascent cells. But we have here to encounter two objections which apply not only to the re-growth of a part, or of a bisected individual, but to fissiparous generation and budding. The first objection is that the part which is reproduced is in the same stage of development as that of the being which has been operated on or bisected; and in the case of buds, that the new beings thus produced are in the same stage as that of the budding parent. Thus a mature salamander, of which the tail has been cut off, does not reproduce a larval tail; and a crab does not reproduce a larval leg. In the case of budding it was shown in the first part of this chapter that the new being thus produced does not retrograde in development,—that is, does not pass through those earlier stages, which the fertilised germ has to pass through. Nevertheless, the organisms operated on or multiplying themselves by buds must, by our hypothesis, include innumerable gemmules derived from every part or unit of the earlier stages of development; and why do not such gemmules reproduce the amputated part or the whole body at a corresponding early stage of development?

The second objection, which has been insisted on by Delpino, is that the tissues, for instance, of a mature salamander or crab, of which a limb has been removed, are already differentiated and have passed through their whole course of development; and how can such tissues in accordance with our hypothesis attract and combine with the gemmules of the part which is to be reproduced? In answer to these two objections we must bear in mind the evidence which has been advanced, showing that at least in a large number of cases the power of re-growth is a localised faculty, acquired for the sake of repairing special injuries to which each particular creature is liable; and in the case of buds or fissiparous generation, for the sake of quickly multiplying the organism at a period of life when it can be supported in large numbers. These considerations lead us to believe that in all such cases a stock of nascent cells or of partially developed gemmules are retained for this special purpose either locally or throughout the body, ready to combine with the gemmules derived from the cells which come next in due succession. If this be admitted we have a sufficient answer to the above two objections. Anyhow, pangenesis seems to throw a considerable amount of light on the wonderful power of re-growth.

It follows, also, from the view just given, that the sexual elements differ from buds in not including nascent cells or gemmules in a somewhat advanced stage of development, so that only the gemmules belonging to the earliest stages are first developed. As young animals and those which stand low in the scale generally have a much greater capacity for re-growth than older and higher animals, it would also appear that they retain cells in a nascent state, or partially developed gemmules, more readily than do animals which have already passed through a long series of developmental changes. I may here add that although ovules can be detected in most or all female animals at an extremely early age, there is no reason to doubt that gemmules derived from parts modified during maturity can pass into the ovules.

With respect to hybridism, pangenesis agrees well with most of the ascertained facts. We must believe, as previously shown, that several gemmules are requisite for the development of each cell or unit. But from the occurrence of parthenogenesis, more especially from those cases in which an embryo is only partially formed, we may infer that the female element generally includes gemmules in nearly sufficient number for independent development, so that when united with the male element the gemmules are superabundant. Now, when two species or races are crossed reciprocally, the offspring do not commonly differ, and this shows that the sexual elements agree in power, in accordance with the view that both include the same gemmules. Hybrids and mongrels are also generally intermediate in character between the two parent-forms, yet occasionally they closely resemble one parent in one part and the other parent in another part, or even in their whole structure: nor is this difficult to understand on the admission that the gemmules in the fertilised germ are superabundant in number, and that those derived from one parent may have some advantage in number, affinity, or vigour over those derived from the other parent. Crossed forms sometimes exhibit the colour or other characters of either parent in stripes or blotches; and this occurs in the first generation, or through reversion in succeeding bud and seminal generations, of which fact several instances were given in the eleventh chapter. In these cases we must follow Naudin,[57] and admit that the "essence" or "element" of the two species,—terms which I should translate into the gemmules,—have an affinity for their own kind, and thus separate themselves into distinct stripes or blotches; and reasons were given, when discussing in the fifteenth chapter the incompatibility of certain characters to unite, for believing in such mutual affinity. When two forms are crossed, one is not rarely found to be prepotent in the transmission of its characters over the other; and this we can explain by again assuming that the one form has some advantage over the other in the number, vigour, or affinity of its gemmules. In some cases, however, certain characters are present in the one form and latent in the other; for instance, there is a latent tendency in all pigeons to become blue, and, when a blue pigeon is crossed with one of any other colour, the blue tint is generally prepotent. The explanation of this form of prepotency will be obvious when we come to the consideration of Reversion.

When two distinct species are crossed, it is notorious that they do not yield the full or proper number of offspring; and we can only say on this head that, as the development of each organism depends on such nicely-balanced affinities

[57] See his excellent discussion on this subject in 'Nouvelles Archives du Muséum,' tom. i. p. 151.

between a host of gemmules and nascent cells, we need not feel at all surprised that the commixture of gemmules derived from two distinct species should lead to partial or complete failure of development. With respect to the sterility of hybrids produced from the union of two distinct species, it was shown in the nineteenth chapter that this depends exclusively on the reproductive organs being specially affected; but why these organs should be thus affected we do not know, any more than why unnatural conditions of life, though compatible with health, should cause sterility; or why continued close interbreeding, or the illegitimate unions of heterostyled plants, induce the same result. The conclusion that the reproductive organs alone are affected, and not the whole organisation, agrees perfectly with the unimpaired or even increased capacity in hybrid plants for propagation by buds; for this implies, according to our hypothesis, that the cells of the hybrids throw off hybridised gemmules, which become aggregated into buds, but fail to become aggregated within the reproductive organs, so as to form the sexual elements. In a similar manner many plants, when placed under unnatural conditions, fail to produce seed, but can readily be propagated by buds. We shall presently see that pangenesis agrees well with the strong tendency to reversion exhibited by all crossed animals and plants.

Each organism reaches maturity through a longer or shorter course of growth and development: the former term being confined to mere increase of size, and development to changed structure. The changes may be small and insensibly slow, as when a child grows into a man, or many, abrupt, and slight, as in the metamorphoses of certain ephemerous insects, or, again, few and strongly-marked, as with most other insects. Each newly formed part may be moulded within a previously existing and corresponding part, and in this case it will appear, falsely as I believe, to be developed from the old part; or it may be formed within a distinct part of the body, as in the extreme cases of metagenesis. An eye, for instance, may be developed at a spot where no eye previously existed. We have also seen that allied organic beings in the course of their metamorphoses sometimes attain nearly the same structure after passing through widely different forms; or conversely, after passing through nearly the same early forms, arrive at widely different mature forms. In these cases it is very difficult to accept the common view that the first-formed cells or units possess the inherent power, independently of any external agency, of producing new structures wholly different in form, position, and function. But all these cases become plain on the hypothesis of pangenesis. The units, during each stage of development, throw off gemmules, which, multiplying, are transmitted to the offspring. In the offspring, as soon as any particular cell or unit becomes partially developed, it unites with (or, to speak metaphorically, is fertilised by) the gemmule of the next succeeding cell, and so onwards. But organisms have often been subjected to changed conditions of life at a certain stage of their development, and in consequence have been slightly modified; and the gemmules cast off from such modified parts will tend to reproduce parts modified in the same manner. This process may be repeated until the structure of the part becomes greatly changed at one particular stage of development, but this will not necessarily affect other parts, whether previously or subsequently formed. In this manner we can understand the remarkable independence of structure in the successive metamorphoses, and especially in the successive metageneses of many animals. In the case, however, of diseases which supervene during old age, subsequently to the ordinary period of procreation, and which, nevertheless, are sometimes inherited, as occurs with brain and heart complaints, we must suppose that the organs were affected at an early age and threw off at this period affected gemmules; but that the affection became visible or injurious only after the prolonged growth, in the strict sense of the word, of the part. In all the changes of structure which regularly supervene during old age, we probably see the effects of deteriorated growth, and not of true development.

The principle of the independent formation of each part, owing to the union of the proper gemmules with certain nascent cells, together with the superabundance of the gemmules derived from both parents, and the subsequent self-multiplication of the gemmules, throws light on a widely different group of facts, which on any ordinary view of development appears very strange. I allude to organs which are abnormally transposed or multiplied. For instance, a curious case has been recorded by Dr. Elliott Coues[58] of a monstrous chicken with a perfect additional *right* leg articulated to the *left* side of the pelvis. Gold-fish often have supernumerary fins placed on various parts of their bodies. When the tail of a lizard is broken off, a double tail is sometimes reproduced; and when the foot of the salamander was divided longitudinally by Bonnet, additional digits were occasionally formed. Valentin injured the caudal extremity of an embryo, and three days afterwards it produced rudiments of a double pelvis and of double hind-limbs.[59] When frogs, toads, &c., are born with their limbs doubled, as sometimes happens, the doubling, as Gervais remarks,[60] cannot be due to the complete fusion of two embryos, with the exception of the limbs, for the larvæ are limbless. The same argument is applicable[61] to certain insects produced with multiple legs or antennæ, for these are metamorphosed from apodal or antennæ-less larvæ. Alphonse Milne-Edwards[62] has described the curious case of a crustacean in which one eye-peduncle supported, instead of a complete eye, only an imperfect cornea, and out of the centre of this a portion of an antenna was developed. A case has been recorded[63] of a man who had during both dentitions a double tooth in place of the left second incisor, and he inherited this peculiarity from his paternal grandfather. Several cases are known[64] of additional teeth having been developed in the orbit of the eye, and, more especially with horses, in the palate.

[58] 'Proc. Boston Soc. of Nat. Hist.,' republished in 'Scientific Opinion,' Nov. 10, 1869, p. 488.

[59] Todd's 'Cyclop. of Anat. and Phys.,' vol. iv., 1849–52, p. 975.

[60] 'Compte Rendus,' Nov. 14, 1865, p. 800.

[61] As previously remarked by Quatrefages, in his 'Métamorphoses de l'Homme,' &c., 1862, p. 129.

[62] Günther's 'Zoological Record,' 1864, p. 279.

[63] Sedgwick, in 'Medico-Chirurg. Review,' April, 1863, p. 454.

[64] Isid. Geoffroy Saint-Hilaire, 'Hist. des Anomalies,' tom. i., 1832, pp. 435, 657; and tom. ii. p. 560.

Hairs occasionally appear in strange situations, as "within the substance of the brain."[65] Certain breeds of sheep bear a whole crowd of horns on their foreheads. As many as five spurs have been seen on both legs of certain Game-fowls. In the Polish fowl the male is ornamented with a topknot of hackles like those on his neck, whilst the female has a topknot formed of common feathers. In feather-footed pigeons and fowls, feathers like those on the wing arise from the outer side of the legs and toes. Even the elemental parts of the same feather may be transposed; for in the Sebastopol goose, barbules are developed on the divided filaments of the shaft. Imperfect nails sometimes appear on the stumps of the amputated fingers of man;[66] and it is an interesting fact that with the snake-like Saurians, which present a series with more and more imperfect limbs, the terminations of the phalanges first disappear, "the nails becoming transferred to "their proximal remnants, or even to parts which are not "phalanges."[67]

Analogous cases are of such frequent occurrence with plants that they do not strike us with sufficient surprise. Supernumerary petals, stamens, and pistils, are often produced. I have seen a leaflet low down in the compound leaf of *Vicia sativa* replaced by a tendril; and a tendril possesses many peculiar properties, such as spontaneous movement and irritability. The calyx sometimes assumes, either wholly or by stripes, the colour and texture of the corolla. Stamens are so frequently converted into petals, more or less completely, that such cases are passed over as not deserving notice; but as petals have special functions to perform, namely, to protect the included organs, to attract insects, and in not a few cases to guide their entrance by well-adapted contrivances, we can hardly account for the conversion of stamens into petals merely by unnatural or superfluous nourishment. Again, the edge of a petal may occasionally be found including one of the highest products of the plant, namely, pollen; for instance,

[65] Virchow, 'Cellular Pathology,' 1860, p. 66.

[66] 'Müller's Phys.,' Eng. Translat., vol. i., 1833, p. 407. A case of this kind has lately been communicated to me.

[67] Dr. Fürbringer, 'Die Knochen etc. bei den schlangenähnlichen Sauriern,' as reviewed in 'Journal of Anat. and Phys.,' May, 1870, p. 286.

I have seen the pollen-mass of an Ophrys, which is a very complex structure, developed in the edge of an upper petal. The segments of the calyx of the common pea have been observed partially converted into carpels, including ovules, and with their tips converted into stigmas. Mr. Salter and Dr. Maxwell Masters have found pollen within the ovules of the passion-flower and of the rose. Buds may be developed in the most unnatural positions, as on the petal of a flower. Numerous analogous facts could be given.[68]

I do not know how physiologists look at such facts as the foregoing. According to the doctrine of pangenesis, the gemmules of the transposed organs become developed in the wrong place, from uniting with wrong cells or aggregates of cells during their nascent state; and this would follow from a slight modification in their elective affinities. Nor ought we to feel much surprise at the affinities of cells and gemmules varying, when we remember the many curious cases given in the seventeenth chapter, of plants which absolutely refuse to be fertilised by their own pollen, though abundantly fertile with that of any other individual of the same species, and in some cases only with that of a distinct species. It is manifest that the sexual elective affinities of such plants—to use the term employed by Gärtner—have been modified. As the cells of adjoining or homologous parts will have nearly the same nature, they will be particularly liable to acquire by variation each other's elective affinities; and we can thus understand to a certain extent such cases as a crowd of horns on the heads of certain sheep, of several spurs on the legs of fowls, hackle-like feathers on the heads of the males of other fowls, and with the pigeon wing-like feathers on their legs and membrane between their toes, for the leg is the homologue of the wing. As all the organs of plants are homologous and spring from a common axis, it is natural that they should be eminently liable to transposition. It ought to be observed that when any compound part,

[68] Moquin-Tandon, 'Tératologie Vég.,' 1841, pp. 218, 220, 353. For the case of the pea, *see* 'Gardener's Chron.,' 1866, p. 897. With respect to pollen within ovules, *see* Dr. Masters in 'Science Review,' Oct. 1873, p. 369. The Rev. J. M. Berkeley describes a bud developed on a petal of a Clarkia, in 'Gard. Chronicle,' April 28, 1866.

such as an additional limb or an antenna, springs from a false position, it is only necessary that the few first gemmules should be wrongly attached; for these whilst developing would attract other gemmules in due succession, as in the re-growth of an amputated limb. When parts which are homologous and similar in structure, as the vertebræ of snakes or the stamens of polyandrous flowers, &c., are repeated many times in the same organism, closely allied gemmules must be extremely numerous, as well as the points to which they ought to become united; and, in accordance with the foregoing views, we can to a certain extent understand Isid. Geoffroy Saint-Hilaire's law, that parts, which are already multiple, are extremely liable to vary in number.

Variability often depends, as I have attempted to show, on the reproductive organs being injuriously affected by changed conditions; and in this case the gemmules derived from the various parts of the body are probably aggregated in an irregular manner, some superfluous and others deficient. Whether a superabundance of gemmules would lead to the increased size of any part cannot be told; but we can see that their partial deficiency, without necessarily leading to the entire abortion of the part, might cause considerable modifications; for in the same manner as plants, if their own pollen be excluded, are easily hybridised, so, in the case of cells, if the properly succeeding gemmules were absent, they would probably combine easily with other and allied gemmules, as we have just seen with transposed parts.

In variations caused by the direct action of changed conditions, of which several instances have been given, certain parts of the body are directly affected by the new conditions, and consequently throw off modified gemmules, which are transmitted to the offspring. On any ordinary view it is unintelligible how changed conditions, whether acting on the embryo, the young or the adult, can cause inherited modifications. It is equally or even more unintelligible on any ordinary view, how the effects of the long-continued use or disuse of a part, or of changed habits of body or mind, can be inherited. A more perplexing problem can hardly be proposed; but on our view we have only to suppose that certain cells become at last structurally modified; and that these throw off similarly modified gemmules. This may occur at any period of development, and the modification will be inherited at a corresponding period; for the modified gemmules will unite in all ordinary cases with the proper preceding cells, and will consequently be developed at the same period at which the modification first arose. With respect to mental habits or instincts, we are so profoundly ignorant of the relation between the brain and the power of thought that we do not know positively whether a fixed habit induces any change in the nervous system, though this seems highly probable; but when such habit or other mental attribute, or insanity, is inherited, we must believe that some actual modification is transmitted;[69] and this implies, according to our hypothesis, that gemmules derived from modified nerve-cells are transmitted to the offspring.

It is generally necessary that an organism should be exposed during several generations to changed conditions or habits, in order that any modification thus acquired should appear in the offspring. This may be partly due to the changes not being at first marked enough to catch attention, but this explanation is insufficient; and I can account for the fact only by the assumption, which we shall see under the head of reversion is strongly supported, that gemmules derived from each unmodified unit or part are transmitted in large numbers to successive generations, and that the gemmules derived from the same unit after it has been modified go on multiplying under the same favourable conditions which first caused the modification, until at last they become sufficiently numerous to overpower and supplant the old gemmules.

A difficulty may be here noticed; we have seen that there is an important difference in the frequency, though not in the nature, of the variations in plants propagated by sexual and asexual generation. As far as variability depends on the imperfect action of the reproductive organs under changed conditions, we can at once see why plants propagated asexually

[69] *See* some remarks to this effect by Sir H. Holland in his 'Medical Notes,' 1839, p. 32.

should be far less variable than those propagated sexually. With respect to the direct action of changed conditions, we know that organisms produced from buds do not pass through the earlier phases of development; they will therefore not be exposed, at that period of life when structure is most readily modified, to the various causes inducing variability in the same manner as are embryos and young larval forms; but whether this is a sufficient explanation I know not.

With respect to variations due to reversion, there is a similar difference between plants propagated from buds and seeds. Many varieties can be propagated securely by buds, but generally or invariably revert to their parent-forms by seed. So, also, hybridised plants can be multiplied to any extent by buds, but are continually liable to reversion by seed,—that is, to the loss of their hybrid or intermediate character. I can offer no satisfactory explanation of these facts. Plants with variegated leaves, phloxes with striped flowers, barberries with seedless fruit, can all be securely propagated by buds taken from the stem or branches; but buds from the roots of these plants almost invariably lose their character and revert to their former condition. This latter fact is also inexplicable, unless buds developed from the roots are as distinct from those on the stem, as is one bud on the stem from another, and we know that these latter behave like independent organisms.

Finally, we see that on the hypothesis of pangenesis variability depends on at least two distinct groups of causes. Firstly, the deficiency, superabundance, and transposition of gemmules, and the redevelopment of those which have long been dormant; the gemmules themselves not having undergone any modification; and such changes will amply account for much fluctuating variability. Secondly, the direct action of changed conditions on the organisation, and of the increased use or disuse of parts; and in this case the gemmules from the modified units will be themselves modified, and, when sufficiently multiplied, will supplant the old gemmules and be developed into new structures.

Turning now to the laws of Inheritance. If we suppose a homogeneous gelatinous protozoon to vary and assume a reddish colour, a minute separated particle would naturally, as it grew to full size, retain the same colour; and we should have the simplest form of inheritance.[70] Precisely the same view may be extended to the infinitely numerous and diversified units of which the whole body of one of the higher animals is composed; the separated particles being our gemmules. We have already sufficiently discussed by implication, the important principle of inheritance at corresponding ages. Inheritance as limited by sex and by the season of the year (for instance with animals becoming white in winter) is intelligible if we may believe that the elective affinities of the units of the body are slightly different in the two sexes, especially at maturity, and in one or both sexes at different seasons, so that they unite with different gemmules. It should be remembered that, in the discussion on the abnormal transposition of organs, we have seen reason to believe that such elective affinities are readily modified. But I shall soon have to recur to sexual and seasonal inheritance. These several laws are therefore explicable to a large extent through pangenesis, and on no other hypothesis which has as yet been advanced.

But it appears at first sight a fatal objection to our hypothesis that a part or organ may be removed during several successive generations, and if the operation be not followed by disease, the lost part reappears in the offspring. Dogs and horses formerly had their tails docked during many generations without any inherited effect; although, as we have seen, there is some reason to believe that the tailless condition of certain sheep-dogs is due to such inheritance. Circumcision has been practised by the Jews from a remote period, and in most cases the effects of the operation are not visible in the offspring; though some maintain that an inherited effect does occasionally appear. If inheritance depends on the presence of disseminated gemmules derived from all the units of the body,

[70] This is the view taken by Prof. Haeckel, in his 'Generelle Morphologie' (B. ii. s. 171), who says: "Lediglich die partielle Identität der specifisch constituirten Materie im elterlichen und im kindlichen Organismus, die Theilung dieser Materie bei der Fortpflanzung, ist die Ursache der Erblichkeit."

why does not the amputation or mutilation of a part, especially if effected on both sexes, invariably affect the offspring? The answer in accordance with our hypothesis probably is that gemmules multiply and are transmitted during a long series of generations—as we see in the reappearance of zebrine stripes on the horse—in the reappearance of muscles and other structures in man which are proper to his lowly organised progenitors, and in many other such cases. Therefore the long-continued inheritance of a part which has been removed during many generations is no real anomaly, for gemmules formerly derived from the part are multiplied and transmitted from generation to generation.

We have as yet spoken only of the removal of parts, when not followed by morbid action: but when the operation is thus followed, it is certain that the deficiency is sometimes inherited. In a former chapter instances were given, as of a cow, the loss of whose horn was followed by suppuration, and her calves were destitute of a horn on the same side of their heads. But the evidence which admits of no doubt is that given by Brown-Séquard with respect to guinea-pigs, which after their sciatic nerves had been divided, gnawed off their own gangrenous toes, and the toes of their offspring were deficient in at least thirteen instances on the corresponding feet. The inheritance of the lost part in several of these cases is all the more remarkable as only one parent was affected; but we know that a congenital deficiency is often transmitted from one parent alone—for instance, the offspring of hornless cattle of either sex, when crossed with perfect animals, are often hornless. How, then, in accordance with our hypothesis can we account for mutilations being sometimes strongly inherited, if they are followed by diseased action? The answer probably is that all the gemmules of the mutilated or amputated part are gradually attracted to the diseased surface during the reparative process, and are there destroyed by the morbid action.

A few words must be added on the complete abortion of organs. When a part becomes diminished by disuse prolonged during many generations, the principle of economy of growth, together with intercrossing, will tend to reduce it still further as previously explained, but this will not account for the complete or almost complete obliteration of, for instance, a minute papilla of cellular tissue representing a pistil, or of a microscopically minute nodule of bone representing a tooth. In certain cases of suppression not yet completed, in which a rudiment occasionally reappears through reversion, dispersed gemmules derived from this part must, according to our view, still exist; we must therefore suppose that the cells, in union with which the rudiment was formerly developed, fail in their affinity for such gemmules, except in the occasional cases of reversion. But when the abortion is complete and final, the gemmules themselves no doubt perish; nor is this in any way improbable, for, though a vast number of active and long-dormant gemmules are nourished in each living creature, yet there must be some limit to their number; and it appears natural that gemmules derived from reduced and useless parts would be more liable to perish than those freshly derived from other parts which are still in full functional activity.

The last subject that need be discussed, namely, Reversion, rests on the principle that transmission and development, though generally acting in conjunction, are distinct powers; and the transmission of gemmules with their subsequent development shows us how this is possible. We plainly see the distinction in the many cases in which a grandfather transmits to his grandson, through his daughter, characters which she does not, or cannot, possess. But before proceeding, it will be advisable to say a few words about latent or dormant characters. Most, or perhaps all, of the secondary characters, which appertain to one sex, lie dormant in the other sex; that is, gemmules capable of development into the secondary male sexual characters are included within the female; and conversely female characters in the male: we have evidence of this in certain masculine characters, both corporeal and mental, appearing in the female, when her ovaria are diseased or when they fail to act from old age. In like manner female characters appear in castrated males, as in the shape of the horns of the ox, and in the absence of horns in castrated stags. Even a slight change in the conditions of life due to confinement sometimes suffices to prevent the development of masculine characters in male animals, although their reproductive organs are not permanently injured. In the many cases in which masculine characters are periodically renewed, these are latent at other seasons; inheritance as limited by sex and season being here combined. Again, masculine characters generally lie dormant in male animals until they arrive at the proper age for reproduction. The curious case formerly given of a Hen which assumed the masculine characters, not of her own breed but of a remote progenitor, illustrates the close connection between latent sexual characters and ordinary reversion.

With those animals and plants which habitually produce several forms, as with certain butterflies described by Mr. Wallace, in which three female forms and one male form co-exist, or, as with the trimorphic species of Lythrum and Oxalis, gemmules capable of reproducing these different forms must be latent in each individual.

Insects are occasionally produced with one side or one quarter of their bodies like that of the male, with the other half or three-quarters like that of the female. In such cases the two sides are sometimes wonderfully different in structure, and are separated from each other by a sharp line. As gemmules derived from every part are present in each individual of both sexes, it must be the elective affinities of the nascent cells which in these cases differ abnormally on the two sides of the body. Almost the same principle comes into play with those animals, for instance, certain gasteropods and Verruca amongst cirripedes, which normally have the two sides of the body constructed on a very different plan; and yet a nearly equal number of individuals have either side modified in the same remarkable manner.

Reversion, in the ordinary sense of the word, acts so incessantly, that it evidently forms an essential part of the general law of inheritance. It occurs with beings, however propagated, whether by buds or seminal generation, and sometimes may be observed with advancing age even in the same individual. The tendency to reversion is often induced by a change of conditions, and in the plainest manner by crossing. Crossed forms of the first generation are generally nearly intermediate in character between their two parents; but in the next generation the offspring commonly revert to one or both of their grandparents, and occasionally to more remote ancestors. How can we account for these facts? Each unit in a hybrid must throw off, according to the doctrine of pangenesis, an abundance of hybridised gemmules, for crossed plants can be readily and largely propagated by buds; but by the same hypothesis dormant gemmules derived from both pure parent-forms are likewise present; and as these gemmules retain their normal condition, they would, it is probable, be enabled to multiply largely during the lifetime of each hybrid. Consequently the sexual elements of a hybrid will include both pure and hybridised gemmules; and when two hybrids pair, the combination of pure gemmules derived from the one hybrid with the pure gemmules of the same parts derived from the other, would necessarily lead to complete reversion of character; and it is, perhaps, not too bold a supposition that unmodified and undeteriorated gemmules of the same nature would be especially apt to combine. Pure gemmules in combination with hybridised gemmules would lead to partial reversion. And lastly, hybridised gemmules derived from both parent-hybrids would simply reproduce the original hybrid form.[71] All these cases and degrees of reversion incessantly occur.

It was shown in the fifteenth chapter that certain characters are antagonistic to each other or do not readily blend; hence, when two animals with antagonistic characters are crossed, it might well happen that a sufficiency of gemmules in the male alone for the reproduction of his peculiar characters, and in the female alone for the reproduction of her peculiar characters, would not be present; and in this case dormant gemmules derived from the same part in some remote progenitor might easily gain the ascendancy, and cause the reappearance of the long-lost character. For instance, when black and white pigeons, or black and white fowls, are crossed,—colours which

[71] In these remarks I, in fact, follow Naudin, who speaks of the elements or essences of the two species which are crossed. *See* his excellent memoir in the 'Nouvelles Archives du Muséum,' tom. i. p. 151.

do not readily blend,—blue plumage in the one case, evidently derived from the rock-pigeon, and red plumage in the other case, derived from the wild jungle-cock, occasionally reappear. With uncrossed breeds the same result follows, under conditions which favour the multiplication and development of certain dormant gemmules, as when animals become feral and revert to their pristine character. A certain number of gemmules being requisite for the development of each character, as is known to be the case from several spermatozoa or pollen-grains being necessary for fertilisation, and time favouring their multiplication, will perhaps account for the curious cases, insisted on by Mr. Sedgwick, of certain diseases which regularly appear in alternate generations. This likewise holds good, more or less strictly, with other weakly inherited modifications. Hence, as I have heard it remarked, certain diseases appear to gain strength by the intermission of a generation. The transmission of dormant gemmules during many successive generations is hardly in itself more improbable, as previously remarked, than the retention during many ages of rudimentary organs, or even only of a tendency to the production of a rudiment; but there is no reason to suppose that dormant gemmules can be transmitted and propagated for ever. Excessively minute and numerous as they are believed to be, an infinite number derived, during a long course of modification and descent, from each unit of each progenitor, could not be supported or nourished by the organism. But it does not seem improbable that certain gemmules, under favourable conditions, should be retained and go on multiplying for a much longer period than others. Finally, on the view here given, we certainly gain some insight into the wonderful fact that the child may depart from the type of both its parents, and resemble its grandparents, or ancestors removed by many hundreds of generations.

Conclusion.

The hypothesis of Pangenesis, as applied to the several great classes of facts just discussed, no doubt is extremely complex, but so are the facts. The chief assumption is that all the units of the body, besides having the universally admitted power of growing by self-division, throw off minute gemmules which are dispersed through the system. Nor can this assumption be considered as too bold, for we know from the cases of graft-hybridisation that formative matter of some kind is present in the tissues of plants, which is capable of combining with that included in another individual, and of reproducing every unit of the whole organism. But we have further to assume that the gemmules grow, multiply, and aggregate themselves into buds and the sexual elements; their development depending on their union with other nascent cells or units. They are also believed to be capable of transmission in a dormant state, like seeds in the ground, to successive generations.

In a highly-organised animal, the gemmules thrown off from each different unit throughout the body must be inconceivably numerous and minute. Each unit of each part, as it changes during development, and we know that some insects undergo at least twenty metamorphoses, must throw off its gemmules. But the same cells may long continue to increase by self-division, and even become modified by absorbing peculiar nutriment, without necessarily throwing off modified gemmules. All organic beings, moreover, include many dormant gemmules derived from their grandparents and more remote progenitors, but not from all their progenitors. These almost infinitely numerous and minute gemmules are contained within each bud, ovule, spermatozoon, and pollen-grain. Such an admission will be declared impossible; but number and size are only relative difficulties. Independent organisms exist which are barely visible under the highest powers of the microscope, and their germs must be excessively minute. Particles of infectious matter, so small as to be wafted by the wind or to adhere to smooth paper, will multiply so rapidly as to infect within a short time the whole body of a large animal. We should also reflect on the admitted number and minuteness of the molecules composing a particle of ordinary matter. The difficulty, therefore, which at first appears insurmountable, of believing in the existence of gemmules so numerous and small as they must be according to our hypothesis, has no great weight.

The units of the body are generally admitted by physiologists to be autonomous. I go one step further and assume that they throw off reproductive gemmules. Thus an organism does not generate its kind as a whole, but each separate unit generates its kind. It has often been said by naturalists that each cell of a plant has the potential capacity of reproducing the whole plant; but it has this power only in virtue of containing gemmules derived from every part. When a cell or unit is from some cause modified, the gemmules derived from it will be in like manner modified. If our hypothesis be provisionally accepted, we must look at all the forms of asexual reproduction, whether occurring at maturity or during youth, as fundamentally the same, and dependent on the mutual aggregation and multiplication of the gemmules. The re-growth of an amputated limb and the healing of a wound is the same process partially carried out. Buds apparently include nascent cells, belonging to that stage of development at which the budding occurs, and these cells are ready to unite with the gemmules derived from the next succeeding cells. The sexual elements, on the other hand, do not include such nascent cells; and the male and female elements taken separately do not contain a sufficient number of gemmules for independent development, except in the cases of parthenogenesis. The development of each being, including all the forms of metamorphosis and metagenesis, depends on the presence of gemmules thrown off at each period of life, and on their development, at a corresponding period, in union with preceding cells. Such cells may be said to be fertilised by the gemmules which come next in due order of development. Thus the act of ordinary impregnation and the development of each part in each being are closely analogous processes. The child, strictly speaking, does not grow into the man, but includes germs which slowly and successively become developed and form the man. In the child, as well as in the adult, each part generates the same part. Inheritance must be looked at as merely a form of growth, like the self-division of a lowly-organised unicellular organism. Reversion depends on the transmission from the forefather to his descendants of dormant gemmules, which occasionally become developed under certain known or unknown conditions. Each animal and plant may be compared with a bed of soil full of seeds, some of which soon germinate, some lie dormant for a period, whilst others perish. When we hear it said that a man carries in his constitution the seeds of an inherited disease, there is much truth in the expression. No other attempt, as far as I am aware, has been made, imperfect as this confessedly is, to connect under one point of view these several grand classes of facts. An organic being is a microcosm—a little universe, formed of a host of self-propagating organisms, inconceivably minute and numerous as the stars in heaven.