CHAPTER V

REVERSION AND ALLIED PHENOMENA

- "A man can never deny his ancestry."-LAWS OF MANU.
- "Evolution ever climbing after some ideal good,

And Reversion ever dragging Evolution in the mud."-Tennyson.

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§ 1. What is meant by Reversion

Most evolutionists—indeed, most naturalists—have ranked reversion as one of the facts of inheritance. Thus Darwin said (1881): "Any character of an ancient, generalised, or intermediate form may, and often does, reappear in its descendants after countless generations." Wallace, Spencer, Galton, and Weismann have all used the concept "reversion" as a convenient way of summing up a universally admitted series of cases, where organisms exhibit ancestral traits which their parents did not possess. As a descriptive term for summing up these cases, the word "reversion" is useful, convenient and, it

seems to us, entirely legitimate. When we go beyond the use of the word as a descriptive term, and use it as implying that the ancestral characters reappear because they are parts of the inheritance, which have been lying latent for generations, and have suddenly been allowed by some liberating stimulus to express themselves in development, we pass from fact to interpretation, from description to theory, and great care is necessary. For the fact that an organism exhibits some peculiarity characteristic of an ancestor does not necessarily imply that this is due to the rehabilitation of latent items in its inheritance. Although we shall seek in this chapter to show that there are reversions in the strict theoretical sense, we shall also point out that many phenomena have been called reversions in a loose descriptive sense which is often misleading. Thus we have much sympathy with Mr. Bateson's remark: "Around the term 'reversion' a singular set of false ideas have gathered themselves. . . . It would probably help the science of biology if the word 'reversion' and the ideas it denotes were wholly dropped, at all events until variation has been studied much more fully than it has yet been" (Materials for the Study of Variation, p. 78).

If we keep the term as a purely descriptive one, there is no doubt as to the occurrence of what may be called "reversions." But difficulties immediately arise when we ask whether all the phenomena so described are really of the same kind, and when we try to interpret them theoretically.

Illustrations.—A recognition of reversionary or atavistic phenomena is ancient. Plutarch gives the case of a Greek married woman who, having given birth to a black child, was brought to justice as an adulteress, and had science enough to allege in her defence that she was descended from an Ethiopian four generations back. This is paralleled by a case reported by De Quatrefages of two Virginian slaves, to whom a perfectly white child was born. "En voyant la couleur de son enfant, elle fut saisie de terreur, . . . mais son mari la rassura, en lui déclarant que son propre frère était blanc."

We do not mean that the instances just mentioned should be

taken as serious pieces of evidence in favour of the reversion theory, but they may serve to hint at the readiness with which the hypothesis of characters lying latent has been adopted. As we shall see, reversions in the strict sense are apparently few and far between.

A foal is sometimes born with a few stripes on its fore-legs, as if reminding us of striped wild horses. A dovecot with carefully bred pigeons was left to itself for some years, after which it was found to contain numerous blue pigeons, resembling in many ways the wild rock-dove (Columba livia). A

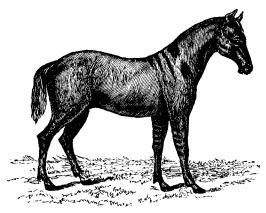


Fig. 25.—Devonshire pony, showing the occurrence of stripes. (From Darwin.)

dark-coloured child may be born in a family where there has been some Eurasian mixture. Cultivated flowers and vegetables, such as pansies and cabbages, sometimes produce forms hardly distinguishable from their wild progenitors. The nectarine derived from a peach may produce what is practically a peach again. The white-flowering currant—derived from the common red form—may have branches with red flowers. These are preliminary illustrations of what are usually called reversions—the hypothesis implied being that they are returns, or "throw-backs," to an ancestral type.

§ 2. Suggested Definitions

Darwin's introductory exposition (1868, vol. ii. p. 28) was as follows: "When the child resembles either grandparent more

closely than its immediate parents, our attention is not much arrested, though in truth the fact is highly remarkable; but when the child resembles some remote ancestor, or some distant member in a collateral line—and we must attribute the latter case to the descent of all the members from a common progenitor—we feel a just degree of astonishment. When one parent alone displays some newly acquired and generally inheritable character, and the offspring do not inherit it, the cause may lie in the other parent having the power of prepotent transmission. But when both parents are similarly characterised, and the child does not, whatever the cause may be, inherit the character in question, but resembles its grandparents, we have one of the simplest cases of reversion."

"The most simple case of reversion—namely, of a hybrid or mongrel to its grandparents—is connected by an almost perfect series with the extreme case of a purely bred race recovering characters which had been lost during many ages; and we are thus led to infer that all the cases must be related by some common bond" (*ibid.* p. 49).

"By the term reversion," Weismann says, "is meant the appearance of characteristics which existed in the more remote ancestors, but were absent in the immediate ancestors—i.e. the parents" (1893, p. 299).

Prof. Karl Pearson defines a reversion as "the full reappearance in an individual of a character which is recorded to have occurred in a definite ancestor of the same race," and atavism as "a return of an individual to a character not typical of the race at all, but found in allied races supposed to be related to the evolutionary ancestry of the given race. . . . In reversion we are considering a variation, normal or abnormal, from the standpoint of heredity in the individual; in atavism we are considering an abnormal variation from the standpoint of the ancestry of the race." But as the two words have been used by some authors in the converse way, and as it is surely difficult to define the field of abnormal variation, we adhere to Darwin's wider usage, and drop the term "atavism" as an unnecessary synonym.

"Reversion," De Vries says, "means the falling back or returning to another type, and the word itself expresses the idea that this latter type is the form from which the variety has arisen. . . . Atavism or reversion is the falling back to a prototype "—i.e. "those ancestors from which a form is known to have been derived." But De Vries distinguishes sharply between true reversion due to a

sudden reassertion of latent ancestral characters in a pure-bred stock, and false reversion or vicinism due to crossing. Descriptively both may be called "reversions," but they differ in their nature and their causes. He also distinguishes reversion to a known ancestor from "systematic atavism" to ancestors which are only reputed to be such on taxonomic grounds.

We would use the term "reversion" to include all cases where, through inheritance, there reappears in an individual some character or combination of characters which was not expressed in his immediate lineage, but which had occurred in a remoter but not hypothetical ancestor. We say "through inheritance" in order to exclude those cases where the reappearance can be accounted for in some other way. There is no reason for complicating the idea by calling the reversionary character "abnormal," for abnormality is often difficult to define.

If we can arrange a series of related types on an inclined plane in order of their evolution, with the most recent highest up, we can imagine the offspring of one of the highest slipping back (as regards one or several of its characters) to a lower level—slipping back beyond the grade represented by its own family or stock, slipping back out of its species-grade altogether, and so forth. These "throw-backs" might be described as family-reversions, stock-reversions, species-reversions, and so on.

§ 3. Theoretical Implications

The general idea behind the term "reversion" is that particular features characteristic of an ancestor may lie dormant—i.e. unexpressed in development—for generations, and may suddenly reassert themselves.

In the mosaic which composes an inheritance there may be included items of ancient origin which can lie latent generation after generation, remaining unexpressed in development for lack of the appropriate liberating stimulus, or for other reasons. Certain potentialities or initiatives, which really form part of

the inheritance and are really transmitted from generation to generation, may be kept under by other components of the inheritance, or in some way prevented from asserting themselves. At length, in the reconstitution which is associated with the maturation and fertilisation of the germ-cells, or in the intimate germinal struggle which is possibly always going on amongst the diverse hereditary items, the long-latent items find their opportunity and the result is a reversion due to the reassertion of long-latent characters. The progeny of the fancy pigeons spoilt by hybridising harks back to its distant ancestor, the rock-dove.

Thus conceived, reversionary phenomena are simply illustrations on a big and striking scale of what is familiarly observed in the common phenomena of "taking after a grandfather" or "skipping a generation." The difference between the case of a boy who has the eyebrows of his great-grandfather, and the case of a domestic pigeon which harks back to the ancestral rock-dove, is simply one of degree. The difference between the occurrence of white spots in some lambs of a herd carefully selected for black wool, and the occurrence of stripes on the forequarters of a Devonshire pony, is simply one of degree. All illustrate ancestral inheritance. But the difference in degree is so marked that a special term—"reversion"—is convenient.

The garden of a shepherd's cottage swallowed up in a deerforest lost all trace of its previous cultivation and became a weed-ground. After many years it was delved, and soon there appeared many different kinds of old-fashioned flowers whose seeds had lain dormant for several generations. So may ancient flowers and weeds now and again reappear out of latency in that garden which we call our inheritance.

§ 4. Phenomena sometimes confused with Reversion

It is impossible to read the fairly abundant literature without becoming convinced that many phenomena are labelled "reversions" on the flimsiest of evidence. The word reminds one of the placard beside a "free toom," "Rubbish Shot Here." It will be no small gain if we can define the conception into one of greater utility by criticism and elimination of alleged instances. In this criticism we have especially to bear in mind that the term "reversion" is not merely descriptive of the direction which variations may take; it implies that this direction—ancestor-wards—is hereditarily determined, that it is due to the reassertion of latent ancestral characters.

After we have sifted out those phenomena whose inclusion under the rubric "reversion" is illegitimate, we shall see more clearly what may be plausibly interpreted as due to the reemergence of ancestral characters after a more or less prolonged period of latency. In regard to the latter it will appear, however, that, although the reversion hypothesis is applicable, other interpretations are not necessarily excluded. Finally, it will be seen that true reversions may arise (a) in a pure-bred race, and (b) much more frequently as the result of hybridisation.

Arrests of Development.—Though popular travesties have reduced a luminous idea to an absurdity, it remains in a general way true that the individual development, especially in the stages of organ-forming, is in some measure a recapitulation of the racial history. Although it is more picturesque than accurate to speak of "every animal climbing up its own genealogical tree," there is a suggestive general resemblance between the stages in the individual development of organs, such as heart, brain, and kidneys, and the stages in the supposed racial evolution of the same.

Now, it not infrequently happens that the recapitulation is notably incomplete, that the development of an organ stops before the normal "finished form" has been attained.

Through defective nutrition or other untoward conditions of nurture, the expression of the inheritance is inhibited. The organism is not able to perfect itself in all its parts; not, we

suppose, through any germinal defect (as subsequent generations may show), but simply because it was not sufficiently fed, or because it was poisoned, and so forth. The results may be congenital, but they are not germinal; they are due to defects not in nature, but in nurture. Thus children born in times of famine are sometimes far below the normal human standard, but it is an assumption to ascribe their deficiencies to their inheritance. In short, all cases of arrested development which can be referred to peculiarities of pre-natal or post-natal nurture should be eliminated from the category of "true inborn reversion." For practical purposes, in rough-and-ready description, they may be called reversions, but they are modificational results; they do not require the hypothesis of the reawakening of latent It is reducing scientific terminology to ancestral characters. an absurdity to describe as a reversion what may be simply due to premature birth or deficient nutrition.

There is a stage in the development of the human fœtus when the openings of the nostrils communicate down the lip with the corners of the mouth-opening; when this communication, which is normally closed up, persists, we have (in part) the abnormality known as "hare-lip," which is normal in rabbit and hare, and is even more clearly seen in the skate and similar fishes. But there is no reason. to interpret the abnormality in man as a reversion; it is an arrest at a stage which is normally passed through; it is probably due simply to a lack of developmental vigour, or more simply still to a lack of adequate nutrition. Dr. Joseph Bell * refers to a case mentioned by Prof. Haughton of young lion-cubs which all died of hare-lip—the supposed reason of the arrest being that the keeper fed the pregnant lioness on tit-bits, without bones. supply of bones was ensured on subsequent occasions, the tendency to hare-lip disappeared.

In a hornless breed of cattle, derived originally from a horned breed, a calf is born with small horns. This may be plausibly interpreted as a reversion to a horned ancestor. But when a calf

^{* &}quot;Discussion on Heredity in Disease," Scottish Med. and Surg. Journ. vi. 1900, p. 307.

is born with a three-chambered heart, it is gratuitous to call this a reversion to the saurians with three-chambered hearts, from which mammals evolved. It is simply a case of arrested development.

Yestigial Structures.—It is a familiar fact that structures of ancient origin and erstwhile importance may still linger in dwindled expression in organisms where they do not seem to have much or any significance. They are relics of the past, vestiges of ancestral history, comparable, as Darwin said, to the unsounded letters in many words, the o in leopard, or the b in doubt—non-functional vestigial letters of which the spelling-reformers would rob us so ruthlessly.

Each one of us is a walking museum of such relics, some of which we should probably do better without. Thus the unused muscles of the ear and the rudimentary third eyelid are ancestral characters which persist in us, though without much significance now. They are like the unused, often unusable, buttons, etc. which survive on some parts of our every-day attire—useless, but interesting, vestiges of bygone days. The gill-clefts of reptiles, birds, and mammals; the embryonic teeth of whalebone whales; the buried remains of pelvis and hind-limbs in whales; the hint of a gill in the skate's spiracle, and so on, are familiar examples of these "vestigial structures," traces of ancestral history, and intelligible on no other theory.

But it goes without saying that as the occurrence of these vestigial structures is still normal, there is no utility in calling them "reversions"—even if now and again they are expressed in greater strength than usual or persist beyond the time at which many of them (e.g. all the gill-clefts save one) disappear—namely, during development. They are very interesting, however, (I) in showing that ancestral features have great power of hereditary persistence, and (2) inasmuch as they often show great variability.

Acquired Modifications resembling Ancestral Characters.— When an individual exhibits a structural peculiarity not expressed in parents or grandparents, but known to occur in more or less remote ancestors, we must try to discover how far this peculiarity is really part of the inheritance. That is to say, we must inquire whether it may not be a modification induced from without, which happens to resemble an innate character of the ancestors. Many domesticated animals which have become wild (feral) may show features resembling the original wild ancestor, but these may be due to the direct influence of the old environment and the old functions. It is safe to say that many of the so-called reversions of feral animals are not inborn but acquired and modificational.

Filial Regression.—We shall afterwards consider (Chapter IX.) Mr. Galton's Law of Filial Regression, but it must be noticed here, if only to point out that it has nothing to do with reversion. The law, concretely stated, is that offspring are not likely to differ from mediocrity in a given direction so widely as their parents do in the same direction. There is a continual tendency to sustain a specific average, or a stock-average.

Let us take a simple instance from Prof. Karl Pearson's Grammar of Science. Suppose a group of fathers with a stature of 72 in.: the mean height of their sons is 70.8 in.—a regression towards the mean height of the general population. On the other hand, fathers with a mean height of 66 in. give a group of sons of mean height 68.3 in.—again nearer the mean height of the general population. The "regression" works both ways; there is a levelling-up as well as a levelling-down. "The father with a great excess of the character contributes sons with an excess, but a less excess of it; the father with a great defect of the character contributes sons with a defect, but less of it."

Now this very important and normal fact of filial regression has nothing to do with reversion, which implies the reappearance of a definite ancestral character or set of characters which have "lain latent" for several generations.

Independent Variations resembling Reversions.-If we

mean by reversion the re-expression of an ancestral character after a period of latency, it is obviously a particular mode of inheritance. From another point of view it is a variation, and due to some unknown germinal conditions which permit a long-latent, but never lost, character to re-assert itself. When we consider the intricate reductions which occur in the maturation of the germcells, and the not less intricate reinforcements involved in amphimixis, it is not impossible to imagine how an ancient latent character may come to the front again after many generations.

But we have also to remember that, apart from reassertions of what is relatively old, there is a continual emergence of what is relatively new. What occurred once as a new variation may occur again, and it is a certain fact that the same type of variation occurs over and over again in varieties of different species. How many red and blue flowers have white varieties! how many trees have weeping varieties! how many Arthropods show similar increase or decrease in the number of their joints! how many birds show albinism! There are limits to the variations of the kaleidoscope, and to the kaleidoscope of variations. Therefore it is always possible that a variation really occurring de novo, and apart from latent characters, may happen to coincide with an ancestral trait. It may be described as a reversion, but it is really an independent variation.

Supernumerary mammæ occasionally occur in human beings in both sexes. Ammon found them in 3 per cent. of German recruits. They obviously suggest the several pairs of mammæ which occur in many mammals—e.g. in the half-monkeys or Lemurs. Weismann (1893, p. 333) says, "They are undoubtedly to be looked upon as reversions to extremely remote characters possessed by our lower mammalian forefathers." But it seems simpler to regard them as independent variations, comparable to many other abnormal multiplications of parts. They happen to suggest bygone conditions, but that is probably all that we are warranted in saying.

Polydactylism in man has been interpreted as a reversion to an

ancestor with more than five digits; but this is illegitimate, for the so-called "heptadactylous ancestor" is a pure myth. Polydactylism in man can only be called a reversion when there is in the family history a previous occurrence of the same abnormality some generations back.

It occasionally happens that a particular part of the skin in man exhibits a mouse-like covering of close-set hair. To interpret this—a mere random variation—as a reversion is credulous in the extreme. It may also be noted, incidentally, that to call the wool-like covering of small hairs (the "lanugo") on the human fœtus a reversion to a hairy ancestor is quite absurd; it is a normal stage in development quite outside the rubric of reversion. It may be an inheritance from a distant past, but it is no more a reversion than the occurrence of a notochord as a constant antecedent to the development of its substitute, the backbone. Similarly the dog's habit of turning round and round before it settles down to sleep may be interpretable in the light of past history, but it has nothing to do with reversion.

"When horses are occasionally born at the present day in which one or two accessory toes are present on two or even all four feet, we are perfectly right in considering the development of these toes to be due to reversion to an ancestor of the Miocene period." That the modern horse which steps daintily on the tip of a single (third) toe for each limb, and has merely hidden rudiments of the second and fourth, has been evolved from a many-toed ancestor, is one of the most certain of evolutionist inferences, but are we "perfectly right" in interpreting the occasional development of supernumerary toes, as on Julius Cæsar's horse, to the reassertion of latent ancestral items in the inheritance? Is it not simpler to regard this as an independent variation, comparable to multiplications of other parts to which reversionary interpretations are inapplicable? We must remember, also, that vestigial organs are in many cases peculiarly liable to vary.

It ought not to be necessary to remark that the ancestor to whom the organism is supposed to revert must be real, not hypothetical.

Some enthusiastic exponents of the reversion theory have not scrupled to name or even invent the ancestor to whom the peculiarity in question is supposed to be a reversion, although evidence of the pedigree is wanting. And the terribly vicious circle is not unknown of arguing to a supposed ancestor from the supposed reversion, and then justifying the term "reversion" by its resemblance to the supposed ancestor. Playing with biology can hardly go further than this! Moreover, the postulate of characters remaining latent (save for occasional more or less hypothetical reawakenings) for millions of years, is made as glibly as if it were just as conceivable as a throw-back to a great-grandfather.

There are many reasons why it is absurd to describe a Cyclopean one-eyed human monster as a reversion to the one-eyed larval ascidian. One is that there is no warrant for believing that the ascidian type was in the direct line of our long pedigree.

One of the diagnostic features of gout is the presence of uric acid in the blood, and its deposition in various tissues of the body (doubtless helped by the frequently associated degeneration of the kidney, which is normally competent to filter out the normal nitrogenous waste-product, which is mostly in the form of urea). It is known, however, that reptiles, for instance, like many backboneless animals. normally excrete most or a large part of their nitrogenous waste in the form of urie acid. This has led even such an eminent pathologist as Prof. Hamilton (1900, p. 297) to say, "May we not entertain, as a possibility, that the gouty constitution, so-called, is in part a reversion to some far-back ancestor, in which uric acid was excreted normally to a much larger extent than it is at present in an average member of the human race?" That is to say, the gouty person reverts to the physiological habit of a far-back ancestral organism (not even any known mammalian type), which had uric acid as a characteristic waste-product, but he does not, unfortunately, revert to the associated condition of having kidneys able to excrete the uric acid adequately. But our simple point is that the supposition of gouty tendencies lying latent in some form or other through literally millions of years taxes our imagination too severely. instances are almost sufficient to damn the reversion hypothesis altogether.

§ 5. "Skipping a Generation"

There is every reason to believe that an individual inheritance is like a mosaic, built up of many contributions, through the two parents, from the grandparents and great-grandparents. It is, therefore, a normal and frequent fact of inheritance that an offspring should re-exhibit the peculiarity of a grandfather, though neither of the parents showed it. There seems little utility in calling a very frequent occurrence like this a reversion, though it is of the same general nature.

It is obviously difficult to decide where it is convenient to draw the line. For how long must a character have been absent—
i.e. latent—before its re-assertion or re-awakening is to be called a reversion? It is a question of convenience, and our view is that it rather obscures the issue to use a special term when the "throw-back" is merely to a grandfather or even great-grandfather. If the term had not been abused it would have been convenient to call these minor family throw-backs "atavisms."

A drone-bee arises from an unfertilised egg; it has a mother and two grandparents, but no father. But it seems rather absurd to call its resemblance to its grandfather either atavistic or reversionary. This is a reductio ad absurdum, for the drone-bee would resemble its father if it had one! But the case may serve to show that it is undesirable to use the term unless the throw-back is to an ancestor more than two generations antecedent.

§ 6. Splitting of Hybrids

We have seen that it is a confusion of thought to associate with reversion what is known as *filial regression*, which is an every-day occurrence in blended inheritance. Similarly, to associate with reversion what is demonstrably due to arrest of development or to inhibitory modificational effects of nurture is a misunderstanding. We have also seen that, for a different

reason, there is no advantage in associating with reversion the common phenomenon known as "skipping a generation" or resembling a grandfather. There is no confusion of thought in the association just mentioned, but it is unnecessary. Reversion is the reassertion of latent characters inherited from a more or less remote ancestor.

In the same way it is unnecessary to complicate the concept of reversion by including the common phenomenon known as the splitting of hybrids. It is now well known that in certain cases the pairing of similar hybrids—e.g. by self-pollination in flowers—is followed by the so-called Mendelian phenomenon, that a definite proportion of the offspring return to the two original parental types. As this is a constant phenomenon in certain well-investigated cases, it seems unprofitable to speak of these as reverting to the parental types. Reversion is an unusual and rare phenomenon, a harking back to a more or less remote ancestor.

A tabby-coloured cat of the Persian breed, crossed with a white male of the same breed, produced four kittens, two tabby-coloured and two white. The two white offspring were interbred and produced four kittens, two pure-white like the sire and grandsire, two tabby-coloured like their grandmother (Ewart). There appear to be many similar phenomena, and it seems in no way advantageous to apply the term "reversion" to what is merely a reassertion of grandparental characters.

§ 7. Reversion in Crosses

False Reversion or Vicinism.—In his criticism of cases which have been labelled "reversions," De Vries draws a sharp distinction between "true reversion," due to unknown internal causes which induce long-lost latent ancestral characters to assert themselves, and "false atavism or vicinism," which is due to crossing. His investigation of a large number of cases led him

to conclude that "true atavism, or reversion caused by an innate latent tendency, seems to be very rare," and that most of the botanical instances are due to crossing. He calls this false reversion "vicinism," as indicating the sporting of a variety under the influence of others in its vicinity. "Crossing and pure variability are wholly distinct groups of phenomena, which should never be treated under the same head, or under the same name." He does not deny in any way the numerous "reversions" which gardeners describe; he simply points out (with much circumstantial evidence to warrant his contention) that nearly all these ordinary "reversions" are due to crosses. shows, for instance, how a famous case, the reversion of the "Tuscarora" variety of American corn cultivated by Metzger in Baden, may be readily interpreted as a typical instance of vicinism. Why the offspring of hybrids should revert to the parental type is another question, to which we shall return in the chapter on Mendelism (Chapter X.).

Two white-flowered sweet-peas are crossed, and the result is a progeny with the wild, purple flowers. Two smooth stocks are crossed, and the result is a progeny with the original hoary, ancestral type. These cases are what Darwin called "reversion on crossing." But, as Mr. Bateson says, "such reversion is nothing but the meeting of two parted complementary elements, which have somehow been separated by variation."

Thus it is possible that many so-called reversions may be simply Mendelian phenomena in disguise.

§ 8. Reversion of Retrogressive Varieties

Within a species it is often possible to distinguish several subspecies or "elementary species" (De Vries), which differ from one another in many characters affecting many organs. Thus in the species called *Draba verna*, or whitlow grass, there are two hundred or so minor groups, like constellations within

constellations. But the species may also include "varieties," more or less sharply distinguished from the rest of the species by apparent absence of some notable specific feature, or, more rarely, by the acquisition of some peculiarity already seen in closely allied species. They stand aside, as it were, like far outlying parts of the constellation. "Varieties," thus defined, usually differ from their parent species in a single sharp character only, or in several correlated characters; they usually arise in a negative way by the apparent loss of some quality; and they have great stability.

Illustrations .--

White "varieties" of red and blue flowers—e.g. of red-flowering currant.

Smooth "varieties" of hairy plants-e.g. nectarine (from peach).

Smooth "varieties" of prickly plants—e.g. holly and gooseberry. Rayless "varieties" of many composites normally with ray-

florets—e.g. white marigold, camomile, daisy.

Radiate "varieties" of many composites permally with pe

Radiate "varieties" of many composites, normally with no ray-florets—e.g. tansy and groundsel.

Red "varieties" of white flowers—e.g. hawthorn.

Red "varieties" of green trees and shrubs—e.g. beech and birch.

Weeping "varieties" of ash, willow, etc.

Starchless seeds—e.g. sugar-corn.

Seedless fruits-e.g. banana and mandarin orange.

Mr. Burbank's stoneless plum.

As these varieties are most frequently in a negative direction, having apparently lost some character which their parent-species possesses, De Vries includes most of them in the term "retrograde varieties." Perhaps "retrogressive varieties" would be a clearer term.

They usually breed true, but some of them are perpetuated asexually—e.g. of course, the seedless fruits. Sometimes, however, the apparently lost ancestral character re-appears, as when the smooth nectarine, a "variety" of peach, becomes

downy, or when the white-flowering currant puts forth red flowers. Such cases may be described as reversions to the specific type, and they can be interpreted only in two ways. Either we have to do with new variations which happen to hit the old mark, or, as seems more probable, latent ancestral characters have re-asserted themselves.

It is a current belief that these "varieties" have a strong tendency to "revert" to the parent species, but, according to De Vries, this is, as regards pure varieties, not of hybrid origin, and ordinarily propagated by seeds, a popular delusion. "In the present state of our knowledge it is very difficult to decide whether or not true reversion occurs in constant varieties. If it does occur it surely does so very rarely, and only under unusual circumstances, or in particular individuals" (1905, p. 155). It must be noticed, however, that De Vries distinguishes true reversion (due to a spontaneous germinal change) from false reversion which is induced by hybridising.

In illustration of the constancy of varieties he cites the wide-spread rayless form of the wild camomile (Matricaria chamomilla discoidea), which is so constant that many botanists have made a species of it. De Vries raised in successive years between 1,000 and 2,000 seedlings, but observed no trace of reversion. Similarly, the rayless "variety" of the common tansy ragwort (Senecio jacobæa) is quite as stable as the radiate species. De Vries also refers to the stability of white strawberries, green grapes, white currants, crisped lettuce, crisped parsley, smooth spinach, white flax, sugar-corn, and strawberries without runners.

Seed-reversion very Rare.—Excluding cases where it is doubtful whether the variety has not a hybrid origin, and is therefore liable to the peculiar phenomenon known as the splitting up of hybrids, excluding also all cases of "sporting varieties," where an apparent reversion might be a mere coincidence in the crowd of variations, De Vries concludes that "seed-reversions must be said to be extremely rare. . . .

It would be bold indeed to give instances of seed-atavism, and I believe that it will be better to refrain wholly from doing so... It is by far safer in the present state of our knowledge to accept bud-variations only as direct proofs of true atavism. And even these may not always be relied on, as some hybrids are liable to split up in a vegetative way, and in doing so to give rise to bud-variations that are in many respects apparently similar to cases of atavism" (1905, p. 176).

§ 9. Interpretations in Terms of Reversion

As in many other cases, one of the difficulties in regard to the reversion theory is that in terms of it much can be interpreted and relatively little demonstrated. In regard to the origins of domesticated animals and cultivated plants, we remain in great obscurity. In regard to the actual pedigree of wild species our ignorance is even greater. Thus, while it is often easy to interpret an unexpected variation as a reversion to a plausible ancestral type, we have little security in so doing.

Thus De Vries distinguishes between experimentally demonstrable reversion and what he calls "systematic atavism," where the ancestral type is merely presumed to be so-and-so on the basis of taxonomic considerations.

It is probable that the common ancestors of the "elementary species" (Primula officinalis, P. elatior, and P. acaulis), which make up the systematic species of primrose, Primula vera, were "perennial plants with a rootstock bearing their flowers in umbels or whorls on scapes. Lacking in Primula vera, these scapes must obviously have been lost at the time of the evolution of this form." But in the common acaulescent "elementary species," P. acaulis, a scape sometimes develops. It may be reasonably interpreted as due to the re-vitalising of a dormant scape-character inherited from the presumed ancestor. "Similarly with the appearance of bracts in the usually bractless

Crucifers, and with the unexpected appearance of upright Similarly, the twisted teasels lose their decussation, but in doing so the leaves are not left in a disorderly dispersion, but a distinct new arrangement takes its place, which is to be assumed as the normal one for the ancestors of the teasel family."

§ 10. Further Examples of Reversion

In one of Prof. Cossar Ewart's experiments a pure white fantail cock pigeon, of old-established breed, which in colour had proved itself prepotent over a blue pouter, was mated with a cross previously made between an owl and an archangel. which was far more of an owl than an archangel. The result was a couple of what were, theoretically, fantail-owl-archangel crosses, but the one resembled the Shetland rock-pigeon, and the other the blue rock of India. Not only in colour (slaty-blue). but in shape, attitude, and movements there was an almost complete reversion to the form which is believed to be ancestral to all the domestic pigeons. The only marked difference was a slight arching of the tail, but there were only twelve tailfeathers, as in the rock-dove, whereas the father fantail had thirty.

A dark bantam hen, crossed with an Indian game Dorking cock, produced amongst others a cockerel almost identical with a jungle fowl (Gallus bankiva)-i.e. with the original wild stock (Ewart).

Similarly, in his horse-zebra hybridisations, Ewart obtained forms whose stripings were at least plausibly interpreted as reversions to an extremely old type of horse, such as is hinted at in the striped ponies of Tibet.

A smooth-coated white rabbit, derived from an Angora and a smooth-coated white buck, was mated with a smoothcoated, almost white doe (grand-daughter of a Himalaya doe), with very interesting results, significant of the complexity of 136

downy, or when the white-flowering currant puts forth red flowers. Such cases may be described as reversions to the specific type, and they can be interpreted only in two ways. Either we have to do with new variations which happen to hit the old mark, or, as seems more probable, latent ancestral characters have re-asserted themselves.

It is a current belief that these "varieties" have a strong tendency to "revert" to the parent species, but, according to De Vries, this is, as regards pure varieties, not of hybrid origin, and ordinarily propagated by seeds, a popular delusion. "In the present state of our knowledge it is very difficult to decide whether or not true reversion occurs in constant varieties. If it does occur it surely does so very rarely, and only under unusual circumstances, or in particular individuals" (1905, p. 155). It must be noticed, however, that De Vries distinguishes true reversion (due to a spontaneous germinal change) from false reversion which is induced by hybridising.

In illustration of the constancy of varieties he cites the wide-spread rayless form of the wild camomile (Matricaria chamomilla discoidea), which is so constant that many botanists have made a species of it. De Vries raised in successive years between 1,000 and 2,000 seedlings, but observed no trace of reversion. Similarly, the rayless "variety" of the common tansy ragwort (Senscio jacobæa) is quite as stable as the radiate species. De Vries also refers to the stability of white strawberries, green grapes, white currants, crisped lettuce, crisped parsley, smooth spinach, white flax, sugar-corn, and strawberries without runners.

Seed-reversion very Rare.—Excluding cases where it is doubtful whether the variety has not a hybrid origin, and is therefore liable to the peculiar phenomenon known as the splitting up of hybrids, excluding also all cases of "sporting varieties," where an apparent reversion might be a mere coincidence in the crowd of variations, De Vries concludes that "seed-reversions must be said to be extremely rare. . . .

It would be bold indeed to give instances of seed-atavism, and I believe that it will be better to refrain wholly from doing so. . . . It is by far safer in the present state of our knowledge to accept bud-variations only as direct proofs of true atavism. And even these may not always be relied on, as some hybrids are liable to split up in a vegetative way, and in doing so to give rise to bud-variations that are in many respects apparently similar to cases of atavism" (1905, p. 176).

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the conditions. In the litter of three, one was the image of the mother, one was an Angora like the paternal grand-



Fig. 26.—Varieties of domestic pigeon arranged around the ancestral rock-dove (Columba livia). (Based on Darwin's figures.)

mother, and the third was a Himalaya like the maternal great-grandmother.

The black polled Angus cattle form a well-marked breed, but the progeny of a perfectly black polled bull and cow is sometimes a red calf with horns; in all probability such a variation is a true reversion traceable to some mixture of stocks a few generations back.

When the swimming-bell or medusoid Epenthesis folleata appears with pentamerous symmetry instead of the usual arrangement of its organs in fours or multiples of four, no one would dream of calling this discontinuous variation an instance of reversion, for we only know of one medusoid (Pseudoclytia bentata) where five is normally the ruling number (Mayer, 1901). But when the last-named medusoid occurs with four oral lips, as it occasionally does, it may be said that this variation is reversionary, since there is good reason to believe that Pseudoclytia pentata is a pentamerous derivative of the Epenthesis stock. Even in this case the interpretation of the four lips as reversionary may not be correct, since, as a matter of fact, the number of lips in Pseudoclytia varies from one to seven.

Reversion in Parthenogenesis.—Weismann (1893, p. 344) reports a very interesting case which he observed in varieties of a small Ostracod crustacean (Cypris reptans) which multiplies parthenogenetically. In the course of observations extending over eight years he found that, amidst the expected uniformity of resemblance between parent and offspring, exceptions occasionally occurred. These were of such a nature that he could only interpret them "as exhibiting reversions to an ancestral form many generations removed."

White-flowering Currant.—The white-flowering variety of the red-flowering currant (Ribes sanguineum) is said to have originated many years ago from seed in Scotland. "Occasionally this whiteflowered currant reverts back to the original red type, and the reversion takes place in the bud. . . . Once reverted, the branches remain for ever atavistic. It is a very curious sight, these small

groups of red branches among the many white ones" (De Vries, 1905, p. 167). This case is peculiar, however, because the white variety is propagated only by cuttings or grafting. "If this is true, all specimens must be considered as constituting together only one individual, notwithstanding their wide distribution in the gardens and parks of so many countries. This induces me to suppose that the tendency to reversion is not a character of the variety as such, but rather a peculiarity of this one individual" (p. 168).

Wheat-ear Carnations.—Large beds of carnations sometimes show peculiar anomalous forms known as "Wheat-ears," with small green ears instead of flowers. There has been a loss of flowers and a multiplication of bracts. On a specimen of this De Vries observed that some branches reverted wholly or partially to the production of normal flowers. "The proof that this retrograde modification was due to the existence of a character in the latent state, was given by the colour of the flowers. If the reverted buds had only lost the power of producing spikes, they would evidently have returned to the characteristics of the ordinary species, and their colour would have been a pale pink. Instead of this, all flowers displayed corollas of a deep brown. They obviously reverted te their special progenitor, the chance variety from which they had sprung, and not to the common prototype of the species" (1905, p. 229).

A Picturesque Case.—The long-headed green dahlia originated twice from two different double-flowered varieties—a deep carmine with white tops on the rays, and a pale orange known as "Sunrise." They were quite sterile and were progagated asexually, one in Prof. De Vries's garden, the other in the nursery at Haarlem, where both arose. "In the earlier cultures both remained true to their types, never producing true florets. No mark of the original difference was to be seen between them." But in 1903 both reverted to their prototypes, and bore ordinary double flower-heads. far we have an ordinary case of reversion. But the important side of the phenomenon was, that each plant exactly 'recollected' from which parent it had sprung. All of those in my garden reverted to the carmine florets with white tips, and all of those in the nursery to the pale orange colour and the other characteristics of the 'Sunrise' variety" (1905, p. 231). It seems impossible not to admit that characters of the parent-varieties had lain for a time latent and had eventually reasserted themselves.

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CONCLUSION.—In his Locksley Hall Sixty Years After Tennyson spoke of—

Evolution ever climbing after some ideal good, And Reversion ever dragging Evolution in the mud;

but this is making a bogey of reversion. Most of the phenomena commonly labelled as "reversions" are wrongly labelled, unless we are content to use the term in a very loose descriptive sense. True reversion does not seem to be of frequent occurrence. Moreover, when it does occur, it may mean, not a deterioration, but a return to a position of greater organic stability. What acts as a drag or brake—often advantageously—on progressive variation is not so much reversion as filial regression.