IX.

Retrogressive Development in Nature.

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EVOLUTION in the animal and vegetable kingdoms is generally understood to mean an uninterrupted progress from lower to higher forms of life. Such a view is not, however, strictly correct; for retrogression plays an important part in evolution, as is shown by the fact that an investigation into the history of degenerate forms often teaches us more of the causes of change in organic nature than can be learnt by the study of progressive ones. Such investigation is, therefore, of the deepest interest.

To begin with a well-known instance, we are all aware of the existence of birds which cannot fly, and of some among them which do not even possess wings. One of these is the Apteryx of New Zealand, called by the natives 'Kiwi-kiwi.' The most superficial observer would at once remark that this bird lacks something, since it reminds one of a man without arms; for the wings are totally absent, and the place where they should be, is covered with a close smooth growth of hair-like feathers.

Not very long ago the question why this bird should lack wings would have been regarded as sufficiently answered by reference to its mode of life. The Kiwi lives in woods, not in the trees, but on the ground; in the day-time it hides in holes in the ground, and comes out warily at night to hunt the worms and insects which form its prey. It has no need of wings to obtain its food, nor does it stand in any fear of native enemies on the ground; for two species of bat are the only representa-

tives of the Mammalia in New Zealand. In former days it would have been said that the Kiwi was created without wings, because it had no need for them ; but now that we can no longer hold the old simple doctrine of special creation, and are compelled to believe that the animals and plants of every age have not been suddenly created out of nothing, but have been developed from ancestral forms, such an assumption can have but little weight. The idea of such special creation is not compatible with the present state of our knowledge; we cannot suppose that the cause of all being called the forms of life into existence in their present form by word alone, but rather by the action of natural forces upon matter, these working together to produce the whole universe of everlasting change, seen in the rise and decline of solar systems, no less than in the evolution and extinction of species. We do not hold that the Kiwi was created out of nothing, but that it was developed from older forms, from species of birds very unlike itself. These birds again were evolved from lizard-like reptiles, which possessed fore- as well as hind-limbs : hence the primitive birds must have had these also, and their fore-legs must have been gradually changed into wings. It is, therefore, certain that the ancestors of the Kiwi possessed wings. Why, then, should the Kiwi have lost them?

Furthermore we have positive evidence in support of the above conclusion that the ancestral form possessed wings, which have been eliminated in the existing species—because the Kiwi even now bears traces of them as minute rudiments hidden under its feathers, and although these no longer serve any purpose, the essential structure of the wing is plainly recognizable, and there are even some short crooked feathers which, with their strong shafts, are very like true primary quills.

The actual reason why the Kiwi possesses only rudimentary wings is, of course, to be found in the fact that, with its present structure and habits, they would be useless to it, and so far we should be justified in saying that the bird has no wings because it has no use for them. The Kiwi is certainly formed for terrestrial life; its short but strong legs and feet are adapted for scratching the earth or digging out holes under the roots of great trees, and enable it to make its escape swiftly and noise-

lessly, when pursued by the natives or by one of the few indigenous birds of prey. It confines itself almost entirely to the food it can find in the earth, especially worms, in searching for which it is greatly assisted by the long beak with its delicate sense of touch. It drives its bill into the soft damp ground, much as the snipe does, and extracts the worms with great skill and precision.

When the species first arose, it was confined to the ground, since nothing was to be gained by leaving it, and the physical structure was therefore adapted to this mode of life, by the gradual elimination of the wings. If the species were only now being formed, the above-mentioned change would most probably not have occurred; for with the invasion of its domain by man, bringing his fire-arms and his cats and dogs, the conditions of life of the Kiwi have been considerably altered, and wings might now stand the helpless bird in good stead. But they have been irretrievably lost, and the race of Kiwis will consequently soon be extinct, like the gigantic ostrich-like birds, the Moas, which are known to have inhabited New Zealand within the memory of man, and the skeletons of which, over twelve feet high, arouse our wonder in museum collections.

As the winged ancestors of the Kiwi adapted themselves more and more to life on the ground in the woods, they came to use their wings less and less, and we may safely conclude that this increasing tendency to disuse of the organs of flight, continuing through long generations, affected the organs themselves, and in some indirect way diminished their size, gradually reducing them to the insignificant appendages we now find.

It is easy to understand how it is that degeneration has gone further in the case of the Kiwi than in that of the ostrich; for, although the latter does not fly, it still uses its wings as aids in running swiftly over the African plains and deserts, while such rapid movement across open country is not necessary for the Kiwi, living as it does in coverts. Short wings with large feathers, like those of the ostrich, would be rather a hindrance than otherwise to the Kiwi in moving quickly through thickets and among underwood, and therefore its wings have been reduced to mere rudiments which are externally altogether invisible.

It is not only among the ostriches that we find degeneration of this kind; certain species of water-birds have become too heavy and awkward to rise into the air, and in these too, for instance in the penguin, the wings are quite useless as organs of flight. But, although useless for flying, they are still of some service for motion in water, and therefore have not degenerated as completely as those of the Kiwi. They have, however, become far smaller than those of flying birds, and, clothed with short scale-like feathers, they bear some resemblance to the fins of fishes.

These few instances will suffice to show that nature is purposeful, not only in adapting recently developed structures to her uses, i. e. in fitting them to perform properly the functions allotted to them, but, conversely, in removing everything superfluous, so that as soon as a structure is no longer required it is eliminated. Of course, this elimination is neither sudden nor voluntary, but comes to pass gradually, in accordance with certain laws, so that we are often able to watch every stage of the transition from the full development of an organ to the entire absence of it.

Such degeneration of once important parts is not only found here and there in nature; it is of frequent, nay, among the higher animals, of general occurrence. It is in fact a natural consequence of the evolution of the higher animals of to-day from earlier and lower forms, which lived under totally different conditions, necessitating the possession of parts and organs, which, in process of time, have been either altered or completely atrophied. If nature had not possessed the power to cause the disappearance of superfluous organs, there could have been no such thing as the transmutation of species; for primitive structures, when they became superfluous, would have been in the way of those in actual use and would have hindered their development. Indeed, had the retention of all original structures been a necessity from the first, the result would have been the production of monsters quite unfit to live. Hence the retrogression of superfluous structures is a condition of progression.

Having found disuse to be the immediate cause of the disappearance of a structure in the course of the development of a species, we may further ask how a structure once essential to

life can fall into disuse. Obviously, this can only happen through a change in the conditions under which the animal lives. When a bird which has been accustomed to seek its food in trees and bushes, finds upon the ground supplies so rich as to afford better sustenance, it will gradually come to live more and more upon the ground, and less and less in trees, a fact which taken alone will entirely alter the conditions of its life. It will not require to fly, and will consequently fly less and less often, and after the lapse of generations will cease to fly altogether. And to bring all this about, the wood in which it lives, the climate, the surrounding animals, need not have undergone any changes; merely the adoption of a new habit by the bird itself will suffice.

It is the same with animals removed from their original habitat; they may find themselves in circumstances so essentially different as to render superfluous some organ which had once been indispensable. For instance, if a species which had always lived in the light, were to find its way into some new habitat where there was complete darkness, its eyes would become useless to it; and accordingly we commonly find that in such species the eyes have more or less completely atrophied.

This is the case, for instance, with animals which live in dark caves. In the limestone caverns of Carniola and Carinthia a blind amphibian, the Proteus, is found in great numbers, and there are also blind Crustacea (both isopods and amphipods), blind insects and snails. In the Mammoth Cave of Kentucky among other blind animals we find a blind fish and a blind fresh-water crayfish. It is almost superfluous to offer any further proof that these species are descended from ancestors which possessed the power of sight, beyond the fact that the caverns in question have not existed from the beginnings of organic life, and that therefore the animals must have lived in the light before they entered them. Nevertheless, in many of these animals direct proof exists in the fact that they still possess vestiges of what have once been eyes. The Proteus and the blind fish of the Mammoth Cave have small imperfectly-developed eyes under the skin, which are no longer of any use as organs of sight. In the case of the blind crayfish, the eyes have entirely disappeared, although the moveable stalks upon which they were placed still remain.

Caves are not the only places where animals are known to live in the dark; in deep wells and at the bottom of the sea and of lakes complete darkness reigns. To Professor Forel of Morges we owe the discovery of the depth to which light can penetrate. Photographic plates were sunk at night to a certain depth, and after being suspended to a buoy, were exposed, for a period of from twenty-one to twenty-four hours, to such light as could reach them. By this means Forel found that even in the transparent water of the Lake of Geneva, the light in winter, when the water is clearest, only penetrated to a depth of 100 metres, and scarcely 50 metres in summer. Later experiments by Fol and Sarasin, with more perfect apparatus and more highly sensitive plates, proved, however, that light penetrates the Lake of Geneva to the greater depth of 170 metres. On a bright day there is about as much light at such a depth as we are accustomed to see on a starlight night, when there is no moon. Below this there is utter darkness; and we find blind animals from these downwards to the greatest depths (300 metres), at which, for example, a blind isopod and an amphipod exist. In the sea, when the water is undisturbed, light penetrates as far as 400 metres, but as we now know that animal life exists in the sea at a depth of 4000 metres, there still remains a vast region in which darkness reigns, and in which numberless blind animals are found,—blind fish, blind crustaceans of various species, blind molluscs and worms. Forms nearly related to all these live where the light penetrates, and possess eyes.

*Burrowing animals, too, have, for the most part, either poorly-*developed eyes or none at all. Thus earthworms are sightless, while closely-allied pelagic species generally possess eyes, often very highly developed, and of complex structure. The common mole has indeed eyes, although very small ones, completely hidden in its close fur, but in Africa there are moles which are devoid of eyes and therefore entirely blind.

Many other instances might be brought forward to prove that the disuse of the organs of vision results in their disappearance. *And the same conclusion holds good for other organs;* experience teaches that, as soon as any organ falls into disuse, it degenerates and is finally lost altogether.

We find interesting confirmation of this fact in the other

organs of special sense, although cases of the disuse of these are of less frequent occurrence. Thus the caecilians, tropical worm-like or snake-like amphibians, living underground, have lost not only the sense of sight, but that of hearing also. They possess neither tympanum nor tympanic cavity, and although the auditory vesicle, which is buried in the interior of the skull, still exists, the auditory nerve, which should be in connection with it, supplying its sensitive nerve-endings, has entirely disappeared. The sense of hearing must have become useless to them in their life underground, or the organ would not have degenerated [1]. They are compensated for the want of it by a remarkably keen sense of smell, which is more highly developed in these animals than in any other vertebrates.

Instances are also known of disuse causing degeneration in the sense of smell; thus the whales and dolphins have more or less completely lost this organ which is so highly developed in the rest of the Mammalia.

Retrogression is, however, not always carried so far as to do away with a structure altogether, although this generally happens with the organs of sense, because they can scarcely be adapted to other uses. But not infrequently the degenerating organ can be turned to account in some other way, and then

[1] It is now known that the above statements as to the existence of a rudimentary auditory organ in *Caecilia* are erroneous. Recent researches have shown us that these animals not only possess a complete auditory apparatus, but that it is even more perfect than in other Amphibia. In their splendid 'Ergebnisse zoologischer Forschungen auf Ceylon,' Heft 4, 1890, the cousins Sarasin have given an accurate account of the auditory organ of a caecilian (*Epicrium*), and show that it is very far from being in a degenerate condition. It possesses all the essential parts, the auditory nerve is even larger than usual, and one of the '*maculae acusticae*' present is unrepresented in other Amphibia. These writers even prove that, in addition to the ordinary apparatus, many accessory auditory organs are present in the skin, each of which contains an otolith: these are homologous with the 'organs of the lateral line' of other Amphibia and of fish.

Up to the present time our knowledge of the auditory organ of *Caecilia* has been founded upon the statements of two excellent observers, Professors Retzius and Wiedersheim; but the material at their disposal was restricted to a few badly preserved specimens.

We must therefore maintain that the organ of hearing as well as that of smell has been especially developed in the caecilians as a compensation for the want of eyesight. Those conditions of life that would render the power of hearing useless do not appear to exist. As a result of these recent researches, I am now unable to adduce an example of a rudimentary auditory organ.—A.W., 1891.

retrogression either stops just short of actual elimination, as in the case of the wings of the ostrich, or so alters and transforms the structure as to fit it for new functions, like the wings of the penguin, which aid it in swimming.

The far-reaching effects, on the development of species, of retrogression consequent upon disuse are nowhere to be seen more clearly than among parasitic animals.

Many groups of animals contain certain genera, families, or even whole orders, which live at the expense of other animals, feeding on their blood or tissues, yet not killing them after the manner of beasts of prey. Such are the parasites, some of which only seek their unwilling host when impelled by hunger, and leave it as soon as they are satisfied; while others take up their abode in or upon it, only to be driven thence by its death. The great group of worms includes very many parasites, and they are almost as numerous among the Crustacea. Most crustaceans are free-swimming or actively running inhabitants of the water, especially of the sea, and their food is partly of a vegetable nature and partly consists of living or dead animals; but nearly every order includes some parasitic form, in which the effects of disuse resulting from parasitism are plainly traceable.

A visit to the fish-market at any European sea-port, and an examination of some of the larger fish, will generally lead to the discovery of certain segmented animals firmly attached to the integument, and bearing some resemblance to wood-lice. These parasites, called fish-lice, suck the blood of the fish. They are not permanently fixed, but leave their host from time to time and seek a fresh one. Now these animals exhibit with great clearness the effects of parasitic habits: their legs are short, being no longer required for swimming, but chiefly for holding on by, and the organs of sense also are somewhat degenerate, for parasites scarcely need them. It is, of course, necessary for predaceous crustaceans to be able to distinguish their prey at a distance, and for this purpose they require keen sight and a delicate sense of touch in their antennae; but parasitic forms, when once attached to their host, do not readily leave it, or if they do so, a new host is easily found, since fish are mostly gregarious. Hence in these fish-lice the eyes and antennae have become small and insignificant.

This is, however, but the first step in retrogressive development: more marked effects are witnessed in forms which are more completely and permanently fixed to their hosts. To the same crustacean order belong the *Entoniscidae*, which are internally parasitic upon other crustaceans, especially upon the common shore-crab (*Carcinus maenas*). During their whole life, these parasites never leave the host, nor move from the position they have once taken up within it. They live attached to its liver, sucking the juices; after growing enormously and producing thousands and thousands of eggs, they finally die. It is clear that such a mode of life must render superfluous, and therefore degenerate, many structures which were essential to their free-swimming ancestors. This retrogression takes place to such a degree, and the whole structure of the animal is thereby so modified and altered that they are scarcely recognizable as Crustacea. The characteristic segmentation of the body is entirely lost, and the hard exo-skeleton is replaced by a thin soft skin. The body lengthens to a vermiform shape, acquires peculiar pointed appendages for the reception of the eggs, and becomes colourless, like that of all animals which live in the dark. All these modifications are quite intelligible; the segmentation of the crustacean body facilitates movement, while the hard exo-skeleton serves for the attachment of muscles. The eyes and antennae completely disappear, because the animal lives in darkness, and does not need to see, and because the sense of touch is unnecessary to it after it has once taken up its position. Not a vestige remains of certain mouth-organs which are well developed in allied species; and the legs, of which free-swimming forms have seven thoracic and six abdominal pairs, are reduced in number. The internal organs are also reduced, with the single exception of the ovaries, which increase so much in size that the animal appears like a mere bag of eggs.

It may now be asked how we know this peculiar vermiform being to be a crustacean and an Isopod at all. We know this to be a fact because there are many other parasitic Isopods in which degeneration has not gone so far, and which present well-marked stages of transition from the above-mentioned fish-lice to the *Entoniscidae*. Furthermore, the descent of the *Entoniscidae* from free-swimming forms is clearly proved by

the fact that the young still resemble the latter in the possession of eyes and antennae, segmented bodies, well developed jaws, and numerous legs: in short, in all essential points of structure, they exactly resemble the locomotive forms. The young of the *Entoniscidae* are actually free-swimming organisms, and it is necessary for the perpetuation of the species that they should be so, for how could the parent animal, possessing no organs of locomotion, leave its original host for a fresh one? And yet such a change is essential for the continuance of the species; for in course of time the hosts will die. Under such circumstances the young *Entoniscidae* leave the mother as perfect Isopods, make their way out of the host, and lead a free-moving life in the sea until they find and enter another *Carcinus maenas*: they then undergo a whole series of retrograde changes in rapid succession, and finally attain the remarkable vermiform shape already spoken of. Of course, retrogressive development did not reach anything like this degree at first; it was only attained after the lapse of countless generations, and a passage through many intermediate forms. The original parasitic Isopods lived no doubt, like the fish-lice, attached to the external integument of their host; these were followed by others which took up their abode in the internal cavities of the body, in the respiratory chamber and the alimentary canal. Gradually increasing modification then occurred, as the parasites found their way farther and farther into the internal organs. The *Entoniscidae* are not the most extreme cases of retrogressive development among the parasitic Crustacea; there are species in which not only the legs, antennae, eyes, and segments of the body, but the whole head, and even the stomach, intestines, and mouth disappear; food being taken in through peculiar root-like tubes, which absorb the juices of the host in such a manner as to supply ready made nourishment which needs no digestion. But the *Entoniscidae* afford sufficient proof of the extraordinary effect of the disuse of certain parts in transforming the whole organic structure of a species.

Since we find that disuse of an organ is always followed by its gradual disappearance in the course of many generations, the supposition naturally arises that this decline is the *direct consequence of disuse*, and that the inactivity of an organ is the

immediate cause of its degeneration, a view which has hitherto actually been held, and which at first seems credible enough and even plausible.

It is, of course, a well-known fact, although perhaps the subject has hardly been sufficiently studied, that parts which are much used grow larger and more powerful, while those which are seldom exercised become small and weak. Constant gymnastic exercise will immensely increase the size and strength of the muscles of our arms; while these limbs will lose what strength they once possessed if the muscles are never exerted. The performances of athletes afford us the best examples of the extent to which practice can increase the muscular strength and activity of man; and, on the other hand, those who work at occupations entailing a sedentary life and lack of exercise plainly show the weakening effects of disuse. Experiments prove this still more clearly: when the nerve supplying a muscle is cut, degeneration of the muscle ensues, because its activity is at an end, and the same thing happens with glands, when their functions are disturbed by severing the nerves which supply them. We may accept the general proposition that an organ may be strengthened by exercise, and weakened by a long continued state of inactivity. It is not necessary here to go into the question of how this is brought about, nor has it been as yet completely explained: it is sufficient for our present purpose to know that such is the case.

Since we may take it for granted that disuse of an organ will lead to its degeneration, even in the life-time of a single individual, may we not also conclude that the gradual disappearance of a superfluous structure in the course of generations is due simply to the tendency to degeneration being handed down from one generation to another, and thus gradually intensified to the extent of complete elimination? For supposing disuse to produce infinitely small effects during the life of each individual, yet surely these effects would be cumulative, and in course of generations the organ would gradually diminish in importance, become smaller and weaker, and ultimately disappear altogether.

This explanation, obvious as it may seem to be, cannot be the right one, for there are many facts which are quite incompatible with it.

In the first place, it compels us to assume as a fact what has often been asserted, but never yet proved, viz. *the hereditary transmission of acquired characters.*

It is well known that many mental and physical qualities of parents are transmitted to their children, such as the colour of the eyes and hair, the shape and size of the finger-nails; and not only these but, as everyone knows, even such minute and indefinable physical and mental characteristics as likeness of features, bearing, gait, handwriting, a mild and equable or passionate and irritable temperament. But all these characters are blastogenic, or inherent in the parents; whether they first show themselves early or late, they have existed in the parents in a more or less marked degree and in different combinations, from the beginning. Characters only acquired by the operation of external circumstances acting during the life of the individual, cannot be transmitted. The loss of a finger is not inherited; all the thousand faculties which are gained by the exercise of various organs or of the whole body are purely personal acquirements, and are not handed down to posterity. No case was ever known of a child being able to read without being taught, even though the parents had exercised their faculties in this direction all their lives. Children do not even learn to speak untaught, although not only their parents, but countless generations of ancestors, have exercised and perfected the brain and vocal organs by learning and speaking a language. It may now be considered as satisfactorily established that children of civilized nations, if brought up in a wilderness and cut off from all communication with man, would make no attempt at speech. For proof of this I need not fall back on the not very well authenticated story of the Persian monarch, who is said to have made the cruel experiment of taking twenty new-born children and bringing them up together, without ever allowing them to hear a word of human speech; they are supposed never to have made any sound resembling speech, but to have imitated with great fidelity the bleating of a goat which lived among them. The same thing is told in all the well-known cases of young or adult persons found living in an utterly wild state in the woods, cases which have occurred from time to time up to the last century in Germany, France, England and Russia. Nearly all

these persons are said to have uttered sounds resembling the cries of wild animals with which they had associated, but not one was ever known to speak. When we consider the constant and unremitting practice in speech which we gain in a life-time, whether by speaking aloud or merely by thinking to ourselves, and remember that in spite of the effect of this perpetual exercise for centuries upon the human brain and vocal organs, —the power of speech has not become in the slightest degree fixed or intensified by heredity, I think that we are justified by this one fact alone in altogether doubting whether acquired characters can ever be transmitted in any real sense. Moreover their transmission is quite incompatible with the only theory of heredity which seems to me to be tenable.

But if the results of the exercise of an organ are not inherited, neither can the effects of disuse be handed down. Hence, if this be true, the retrograde changes taking place during the lives of individuals cannot possibly be intensified in the course of generations; for the process of retrogression would have to begin afresh in each generation successively, and thus would never advance any farther than it did in the individuals of the first. We must, then, regard this supposition that degeneration is caused by mere disuse as a mistaken one, and seek a more satisfactory explanation of the facts. I think, moreover, that such an explanation is to be found in what may be called reversed natural selection.

To state my meaning more clearly, Charles Darwin and Alfred Russel Wallace have taught us to understand by 'natural selection' that process of elimination effected by nature itself without the aid of man. Inasmuch as far more individuals are born than can possibly live, only the best are enabled to survive, the best being those which are so formed as to be the 'fittest,' as we say, for the conditions of life in which they are placed. As in each generation only the fittest survive and propagate the species, their qualities only are transmitted, while the less useful qualities of the weaker individuals die out. Each successive generation will therefore consist of individuals better organized than those of the preceding one, and thus useful characters will be gradually intensified from generation to generation, until the greatest possible degree of perfection is reached. Probably this theory

is far from new to many of my readers: it has been so often explained in various well-known works and periodicals, that any further elucidation is unnecessary.

What holds good for the individual as a whole also holds good for each separate organ, inasmuch as the ability of an animal to perform its allotted functions depends on the efficiency of each particular organ: hence, by means of this perpetual elimination of the unfit, every organ is brought to the greatest perfection. On this hypothesis, and on this only, is it possible to explain the wonderful adaptability of the minutest details of structure in animals and plants, and the development of the organic world through the operation of natural forces.

If this view be the true one, if adaptation in all the parts of living forms be truly the result of natural selection, then the same process which produced these adaptations will tend to preserve them, and they will disappear directly natural selection ceases to act. These considerations show why organs which have become superfluous and have fallen into disuse necessarily degenerate and ultimately disappear.

As an example of this, let us take one of the newts, which are so common in our swamps and pools in spring. If we examine its eyes we find that they are not very large, but very highly developed: their structure bears considerable likeness to that of the human eye, and they play a very important part in the life of the animal, which is almost entirely dependent on keenness of vision for finding its prey. It detects at once and snaps at anything in motion: were it not for its eyes, it would infallibly starve. Now these eyes are extremely delicate and complex organs, which have only very gradually,—i. e. in the course of countless generations and of almost endless time,—reached the degree of perfection attained by them in the living newt. The whole series of developmental stages is not indeed known to us; but in other groups of animals we find eyes at every grade of development, and from these we can form some idea of the way in which the gradual improvement of an original simple and imperfect eye took place. The slow but steady progress in development from stage to stage is due, as I believe, to the fact that the eyes of these animals were never all exactly alike, nor all equally keen, and that only those individuals survived in each generation in which the develop-

ment of the eyes was above the average. This process of natural selection would not only gradually produce improvement in the eye, but would also tend to keep the improvement, when gained, up to a certain standard.

Now suppose such a species to have been carried underground by water into a dark cavern. It would only gradually adapt itself to the new conditions and thus be enabled to thrive in the cave: but after the lapse of generations the individuals would have learnt to live in complete darkness, and to distinguish and catch their prey without the aid of sight, and this would be rendered possible by an improvement in other organs, especially those of touch and smell. Thus in course of time a race of newts would be produced perfectly adapted for life in the dark, and for finding food by scent alone and not by sight; and this race would make its way farther and farther underground, and pass its whole life in utter darkness. It is in some such way as this that not only the entrances of caverns, but whole series of caves, connected by subterranean streams, rivers and lakes, like those in the Karst Mountains, near Trieste, have come to be tenanted by animals.

Directly, however, such cave-dwellers became able to exist without using their eyes, degeneration of these organs would set in: as soon as they ceased to be essential to the life of the animal, natural selection would be powerless to affect them, for it would be immaterial whether the eyes of any animal were above or below the standard. Hence the individuals with weaker sight would no longer be eliminated, but would have an equal chance of surviving and propagating their species. Crossing would then take place between individuals with strong and weak eyes, and the result would be a gradual deterioration of the organ. Possibly the process might be accelerated by the circumstance that small and degenerate eyes would be rather an advantage, because their decrease would involve an increase in the powers of other and now more important organs, such as those of touch and smell. But even independently of this, the eye, directly it ceases to be kept up to a certain standard of development by natural selection, will gradually deteriorate, the process being very slow at first, but absolutely sure.

The same simple explanation suffices for *all* cases of retrogressive development, whether of organs or species. On any

other theory many facts are incapable of explanation, even assuming the possibility of the hereditary transmission of acquired characters, such as those produced by disuse.

It is clear that degeneration as a result of disuse can only take place in an organ the activity of which depends upon its exercise, so that a real effect is produced by the discharge of function. The act of seeing involves certain chemical changes in the retina of the eye, and perhaps even in the optic nerve, processes which do not take place when the eye is no longer exposed to light. Flying involves metabolism in the muscles which move the wings, and this also ceases when flight is at an end. So that an actual retrogressive influence is exerted on certain parts of the eye and on the muscles, by disuse. But how can the stamens of a plant be affected by the failure or success of their pollen in finding its way to the stigma of another flower? Yet we know that hermaphrodite flowers sometimes revert to the original condition in which the sexes were separate, and this by the gradual atrophy of the stamens in one flower and the style in another. Whether this particular case is to be explained by the cessation or by the active operation of natural selection, is another question, which we may proceed to consider.

After the anthers, in the course of evolution, have withered away and disappeared, their stalks (the filaments) remain, and are often of considerable height and thickness. Slowly and very gradually these degenerate also: we find them quite long in some species, in others short, while in others again they have completely disappeared, only reappearing now and then in single instances to remind us that they were once of normal occurrence. It is true that the filaments are no longer useful, but how can this fact have any direct effect in causing them to degenerate? Their structure remains the same, the sap circulates in them as before and supplies nourishment to them as well as to the petals and the style. From my point of view the matter is intelligible enough; for the bare filaments which have lost their anthers are in no way essential to the life of the species: natural selection is powerless to affect them and they gradually degenerate.

Even more striking instances are to be found in the animal kingdom. Why have most of our domestic animals lost their

original colouring? Clearly because colour became of little or no importance to them as soon as they were sheltered under the protection of man, while in a wild state it was a great safeguard against detection by their enemies.

Similarly the hairy covering has ceased to be of importance to certain of the Mammalia—and has disappeared. Thus whales and dolphins have a naked skin for the most part entirely devoid of hair, although they are unquestionably descended from hairy ancestors, and even now rudimentary hairs may be detected in certain parts of the body by the aid of the microscope. Obviously, the disappearance of the hairy covering cannot be a direct consequence of disuse, for hair will grow as well, whether its protective warmth be useful or of no importance to the animal. But its disappearance as an indirect consequence of disuse is plain; for as soon as an immense thickness of blubber was developed beneath the skin of the whale, the warmth of an additional covering was unnecessary: the hair becoming superfluous, natural selection ceased to affect it, and degeneration at once set in. If anyone is inclined to doubt whether the direct action of sea-water may not have caused the disappearance of the hair, it is only necessary to point to the group of seals, in which all the smaller species possess a thick coat of fur, while, among the larger kinds, the walrus has but a scanty covering of bristles, because, like the whale, it has developed a layer of blubber, which is amply sufficient to protect its huge body from cold.

Examples of an entirely different kind are afforded by those animals which hide themselves in cases or houses. The hermit-crab partly conceals itself in empty shells, the aquatic larvae of caddis-flies (*Phryganidae*) build cases within which their cylindrical bodies are enclosed, and the larvae of certain small moths (*Psychidae*) do the same. Whenever the body of any such animal is thus partially enclosed in a case, the protected parts are soft and whitish, i. e. more or less colourless, while the exposed parts retain the ordinary hard integument of the Arthropoda and are variously and strongly coloured. Now we may maintain that, in a certain sense, the hard integument of crabs and insects fulfils the 'function' of protecting the soft parts of the animal from injury, but, correctly speaking, this defence is not a real function at all, because the exercise of

function implies activity, while the use of the hard integument can only be of a passive kind. The horny covering itself is not in the least affected, whether it is useful or useless as a defence against stings and bites: such assaults are quite immaterial to it, nor does its condition in any way depend upon the frequency or rarity of attack. Degeneration cannot, then, be the result of the protection afforded to the integument. Inasmuch as the integument of all the three kinds of animals mentioned above only degenerates in those parts which are protected by the case, clearly the only explanation must be that the hard covering is unnecessary for those parts which are otherwise protected, and that consequently natural selection has no power to preserve it.

But the most striking instances are to be found among the social insects, especially the ants. The male and female ants are winged, and at certain times of the year rise into the air in great swarms. Everyone must have seen these swarms filling the air in summer and autumn: they may often be seen on the top of a hill, or surrounding the summit of some tower, alighting on walls and parapets or covering the hats and clothes of people. The males and females, however, form the minority in an ant-community, the greater number being workers—the common wingless ants. Now these workers, in the course of the development of the species, have forfeited their wings as a consequence of disuse, because the power of flight would be useless to them, and they would be exposed to even greater dangers in the air than on the ground. The business of their lives is to forage for food-supplies, and to collect building materials for the nest, but everything which they seek is obtainable on the ground: they have also to feed the larvae and tend the pupae, and to them alone belongs the defence of the nest if attacked. All these tasks bind them to a life on the ground; hence, when in former days, they were being gradually developed from perfect females, they came to use their wings less and less, as they gave themselves up more and more completely to the duties allotted to them. Now, in this case also, it would at first sight seem probable that the long continued disuse produced a certain amount of degeneration in each individual, that this first retrograde change was inherited by the succeeding generation, and gradually intensified by further disuse, and so on. Such a view is, how-

ever, entirely disposed of by a fact which admits of no dispute and cannot be explained away, viz. *the fact that the workers of ants are infertile, and do not propagate their species.* Consequently, it is impossible that the degeneration caused by disuse during individual lives should be handed down, and the elimination of the wings is only explicable on the other theory, which ascribes it to the cessation of the operation of natural selection which ensued when the wings became useless and of no importance. It may certainly be objected that the disappearance of the wings might have taken place before the workers became infertile; but such a supposition cannot be accepted, for reasons which I need not enter upon here. The infertility of workers may also be regarded as a difficulty from my point of view, but it must be remembered that the principle of the elimination of the unfittest does not act directly on the workers, but on their parents, the propagators of the species. In other words, natural selection does not affect the workers themselves, but the parents, and determines their survival according as they produce perfect or imperfect workers.

The process by which the degeneration of superfluous organs takes place may fittingly be called 'universal crossing' (Panmixia), because it implies that not those individuals only in which any particular organ is best developed survive and propagate their species, but that survival is quite independent of the efficiency or non-efficiency of the organ. This process of Panmixia must have had, and must have still great influence on the development of the organic world. The changes wrought by evolution have been and are innumerable, and they by no means always occur in an upward direction, but often—as shown in the case of the parasites—in a downward one, or perhaps most frequently in both directions at once, the change being retrogressive in one part and progressive in another. And very often the former change may actually lead to the latter. We ourselves could hardly have attained so high a degree of intellectual development, had we not forfeited a considerable share of the physical advantages possessed by our remote ancestors. The savage tribes which depend upon the chase, are gifted with a much keener sense of hearing, smell, and sight than we are, and this is not merely the result of constant training, but is also due to the inheritance of more

efficient organs. In this respect civilization has caused degeneration in us, by means of Panmixia, owing to the fact that the well-being of individuals no longer depends upon the highest possible development of their sense-organs. At the present day we are able to make a living equally well, whether our sense of hearing or smell is delicate or the reverse, and even keenness of sight is no longer of decisive importance to us in the struggle for existence. Ever since the invention of spectacles, short-sighted persons—in the higher classes at any rate—experience hardly any greater difficulty in getting a living, than that endured by people with keen sight. In former times a short-sighted soldier or general would have been a sheer impossibility, and so would a short-sighted hunter: in all grades of society short sight used to be a very real disadvantage and an almost complete bar to advancement of any kind. This is no longer the case now; a short-sighted man makes his way in life as successfully as any other, and his defect, if congenital, will be transmitted to his children, and will therefore tend to make hereditary short sight commoner among certain classes. Of course short sight may also be an acquired character, and in such cases it is, I venture to affirm, not transmitted. But I believe that the great prevalence of short sight is not only due to the injuries acquired by over-straining the eyes and continually looking at near objects, but also to Panmixia, or cessation of the action of natural selection,—a law to which we are naturally subject in common with other animals.

Much might be said of the effects of civilization in causing physical degeneration, which indeed appears to be on the increase. Consider for a moment the teeth: the art of dentistry has been brought to such a pitch of perfection, that artificial teeth are now almost to be preferred to natural ones. At any rate no one need die now from insufficient nourishment in consequence of the inability to masticate food, and there is nothing to prevent the transmission of a predisposition to bad teeth to any number of descendants.

Nevertheless we need not fear that civilization will ever lead to utter degeneration in man. The antidote is to be found in the very process which causes the first deterioration of an organ; for obviously such deterioration can only continue as long as it is not injurious to the individual in the struggle for

existence, and when that point is reached natural selection will interfere to prevent further degeneration. To return to our former example, it is quite conceivable that the percentage of persons with hereditary short sight may steadily increase, without seriously affecting the general standard of vision of mankind as a whole, or even that of a single nation or class, because degeneration below a certain point would become a fact of decisive importance to the individual, leading to failure in the struggle for existence. Thus we need not fear the complete loss of our eyes through degeneration, like that which has affected the animals living in the dark and the above-mentioned parasites; and we need not anticipate any serious diminution of our muscular strength, or powers of endurance, or many other qualities.

Hitherto I have only treated of the degeneration of physical characters in consequence of disuse and Panmixia, but the same thing takes place with mental qualities, a fact which need not surprise us when we remember how close is the connection between all mental and physical processes, how the relative size and complexity of the brain is a measure of the degree of intelligence, and how every instinctive action of an animal presupposes a corresponding arrangement of the nervous system which compels a certain action to follow upon a certain stimulus. Hence degeneration of an instinct in an animal must always have been preceded by degeneration of that network of nerve-cells and nerve-fibres in the brain in which the instinctive action had its rise. Retrogression, then, in physical structure is not antagonistic to retrogression in instinct and mental faculty, but mental and physical degeneration rather go hand in hand. Very definite and extensive physical degeneration always implies a corresponding mental deterioration. Those *Entoniscidae* which have lost their eyes, antennae, legs, and jaws, have also degenerated in intelligence, as is but natural in animals which only require to remain still and imbibe nourishment: the whole nervous system of these Crustacea has been reduced to a remarkable degree.

Certain examples are most interesting as tending to prove that retrogression may be confined to one particular instinct, leaving the animal and its powers as a whole quite unaffected. The loss by domestic animals of the instinct to escape is one of

these examples. Almost all wild animals, mammals as well as birds, possess the instinct to escape: they are not only extremely attentive to the slightest sound and smell, and to every movement taking place within their field of vision, but all of them, the predaceous animals not excepted, are continually mindful of their safety, and though not always consciously on the watch, are so to a great extent instinctively. A wild bird flies away at the least sound; a hedgehog which has been surprised, and has rolled itself up, only unrolls itself to run away after the lapse of a considerable time, while the slightest suspicious sound will make it roll up even more tightly. These acts are not the result of reflection, but are purely instinctive, the act of rolling-up being always associated with the perception of sound, so that the former follows instantaneously upon the latter, before the animal has had time to reflect on its meaning, just as we shut our eyes the instant that anything touches them. In the higher animals these movements are certainly under conscious control, i. e. they are capable of suppression, and hence it is that animals in a state of captivity lose the instinct of being startled and of escaping. This instinct is nevertheless deeply implanted in them, and many generations must be passed in domestication before the natural timidity is lost. I believe that the loss is brought about by cessation of the action of natural selection, and a consequent gradual degeneration of the instinct. Of course it is difficult to judge of the amount of influence exercised by custom upon the life of the individual, but it may at least be considered as certain that the young of our domestic fowls, geese, and ducks, have lost much of the instinct to escape possessed by their wild ancestors, and that they would never become quite wild again even if placed under the care of a wild mother from the first.

The length of time which may be necessary before domestication can get the better of this passive kind of wildness, as the instinct to escape may be called, is seen in the case of the guinea-pig. These animals have been domesticated ever since the discovery of South America about 400 years ago,—a period of time which has not sufficed to overcome their natural timidity. Any loud noise will make them start violently and seek to escape, although they may never in their lives have had any experience of real danger: even shortly after birth the same

thing will happen. In these, as with the various species of pheasants which have been domesticated, the young animals are the wildest: the instinct to escape has been inherited almost unaltered, and the process of taming must begin afresh with each individual. The tameness of the adult animal is here still an acquired character, i. e. one acquired during the lifetime of the individual, and is not inherent, or rather, it is not the result of those changes in the potentialities of the germ which are gradually produced by universal crossing. The tameness comes about just as in wild animals taken young, such as foxes, wolves, rats, or finches, all of which are tameable up to a certain point, and become accustomed to the absence of enemies.

It is also interesting to note that loss of the instinct which impels animals to seek their food may sometimes occur. Both food itself and the power of obtaining it are essential to life, and the instinct of seeking food may be looked upon as the first and earliest developed of any: yet it may be partially or even entirely lost. The young of many birds no longer possess the instinct; they open their bills and cry, and they swallow food placed in their mouths, but they have no idea of picking it up if scattered on the floor of their cage; the sight of food does not result in any impulse to eat. At this early period of life such birds have not learned the art of feeding themselves, and this is not unnatural; for they leave the egg in a very undeveloped condition, and their parents feed them by putting food into their mouths. A part of the food-seeking instinct has thus become superfluous and has disappeared. It may be objected that the little creatures are too undeveloped to feed themselves; this is true, and it is the reason why the parents feed them and why their instinct is undeveloped. But many other birds, fowls, for instance, run about directly they are out of the egg and pick up food for themselves; here the food-seeking instinct is unimpaired.

One of the most remarkable cases of degeneration of the food-seeking instinct is found in certain ants. It has been known ever since the beginning of this century that some species of ants keep slaves, for instance, the reddish ant found in the meadows of Switzerland and Alsace (*Polyergus rufescens*). It is not a large but a strong species, which has adopted the

habit of sallying forth in troops from time to time, to make raids upon and plunder the nests of some weaker species, such as the common *Formica fusca.* The object is, however, not to destroy or devour the ants they attack, but merely to carry off the pupae to their own nest, where they receive every care: the workers hatched from them are then employed as servants, or, to use the usual term, as slaves. These slaves, fulfil all the duties of the nest, which would otherwise have fallen to the share of the red workers; they feed the larvae, build galleries and chambers, bring in food-supplies, and even feed their lazy masters! This is no fable, as was once thought, but an ascertained fact, proved to be such early in this century by Huber of Geneva, a celebrated observer of ants, and since fully confirmed by his pupil and successor Auguste Forel, as well as by Sir John Lubbock. I have also convinced myself of the truth of the assertion.

The most curious part of it, however, is that, in consequence of being constantly fed by their slaves, the red ants have entirely forgotten how to procure food for themselves. If they are shut up and supplied with honey, which is their favourite food, they will not touch it, but will suffer hunger, become weak and feeble, and ultimately die of starvation, unless pity is taken upon them and they are given one of their dusky slaves. Directly this is done, the slave falls to work, eats a quantity of the honey, and then proceeds to feed its masters, which are perfectly willing to be saved from starvation in this manner.

Here, then, as in the case of nestlings, the food-seeking instinct and the power of distinguishing food by sight have degenerated, and clearly in consequence of disuse. Inasmuch as a colony of red ants always owns plenty of slaves, the food-seeking instinct has become unnecessary, natural selection has ceased to affect it, and it has gradually died out. Other instincts too have been lost by these red ants in consequence of their habit of keeping slaves; they have quite forgotten the art of nest-building and in part that of tending their young. Other species of ants devote much attention to their pupae, moving them about the nest from time to time, and often carrying them out into the air and sun, and they feed their larvae with the greatest assiduity. But the red slave-making

ants have no such instincts; they care nothing for their own young, and the species would become extinct, if they were suddenly deprived of their slaves. So it is not only among men, that there is a curse upon slavery; even animals become degraded by it.

Other species of slave-making ants are known, and have been carefully studied, in which the degeneration of the masters goes even farther and affects their physical strength. But so much remains unexplained in the life-history of these species, that I will not treat of them here, remarkable as are the observations which have been made about them. All these examples afford further support to our theory of retrogressive development as a result of disuse; for the above-mentioned cases of the degeneration of instinct took place in worker-ants, i.e. in animals which have not the power of propagating their species. Hence the disappearance of the instincts in question cannot be due to the hereditary transmission of any degeneration acquired by individuals in consequence of the fact that they were not required to seek their own living.

In the cases above quoted, the instinct of feeding has not entirely degenerated, but only a part of it has been lost, viz. the instinct of seeking food and the power of recognizing it by sight. Evidence is, however, forthcoming to show that the whole instinct of feeding is sometimes lost, so that actually no hunger is felt and no nourishment taken. This may sound very strange, but it is an undoubted fact that there are animals which absorb as much nourishment in the larval stage as will last them during the rest of their life. Many moths, especially among the Bombyces, possess very degenerate mouth-organs, and so do the *Ephemeridae*: all these take no sort of food. In male Rotifers the alimentary canal is entirely wanting; they have neither mouth, stomach, nor intestine; their lives are of such short duration that the food material with which they begin life is sufficient to sustain them throughout it. There is no luxury in nature; no instinct and no organ in the body can persist unless absolutely essential to the life of the species. Panmixia—in other words, the cessation of the operation of natural selection—removes all that is superfluous, only leaving that which is absolutely necessary.

But, of course, if our theory be the right one, such retro-

gressive development can only take place very gradually: it must require many generations to completely eliminate what is superfluous, and we should expect to find in many animals vestiges of organs and structures once significant, but now on the road to complete obliteration. And this is actually the case, as I have shown above. So-called 'rudimentary' organs are present in numberless cases, and in various animals, and give us some idea of the vast amount of change which every species must have undergone in the course of ages. Of such a kind are degenerate eyes, hidden beneath the skin, as in the Proteus, the golden mole, and the *Caecilia*; the rudimentary wings of the Kiwi, and of many female moths the males of which have well-developed wings; the almost invisible projections near the mouth of the *Ephemeridae*, which are nothing less than degenerate jaws; and a thousand other examples. To the same causes are due the numerous cases in which an organ, fully developed in the ancestors, is wanting in the adult descendant, although present in a rudimentary condition during youth or embryonic life. Thus, the workers of ants are, as before mentioned, wingless, but the vestiges of wings are still to be seen in the larvae, in the form of small disc-like objects beneath the skin, which subsequently disappear. Thus, too, the larvae of bees have lost their legs, because they do not need to crawl about, but live enclosed in a waxen cell in close proximity to their food: although disuse has thus brought them to the condition of footless grubs, in the egg they nevertheless still exhibit vestiges of the legs which their saw-fly-like ancestors must have possessed. Examples like these show that retrogression in an organ, which degenerates from disuse, takes place first in the mature stage, and does not extend to the embryonic stages until much later. An organ may persist in the embryo for thousands of generations after it has been eliminated from the adult organization. The history of evolution affords many well-authenticated instances of organs which persist in a rudimentary condition and never attain a higher development. They are, of course, of the greatest importance as throwing light upon the past history of a species, and are in themselves sufficient proof of the number and diversity of the ancestors of existing species; they show us how intricate and devious are the workings of nature in the evolution of the organic world—now progressive, now retro-

gressive, now concerned with the development of a single structure, and now of a whole organism. Everything that nature has built up with such elaborate care—highly-developed organs of locomotion, limbs fitted to support a certain weight, joints with their complex and yet easy movements, the exquisite balance of muscular strength required for rapid motion on the ground, wings adapted for flying, with all the marvellously adjusted organs which overcome gravity and render rising into the air a possibility, every one of the adaptations by which animals are placed in communication with the outer world which surrounds them,—eyes of the most delicate and complex structure, organs of hearing and smell so wonderfully formed that it has needed long years of the combined researches of all the most eminent naturalists to understand their full significance—each one of these is relinquished, is handed over to a process of gradual destruction, the moment it ceases to be essential to the life of the species.

It would indeed seem as if such a process of development could not justly be called progress, and as far as the individual organ undergoing degeneration is concerned the process is of course retrogressive; but the case becomes different when we regard the organism as a whole. For the end and purpose of all living beings is after all but the existence of each individual: the form assumed, the complexity of structure, the degree of perfection, are all quite immaterial provided that the species be fit to survive: less than fit it cannot be, or it succumbs, neither can it be more so, because no means exist which can enable it to rise beyond the point of fitness necessary for survival. Schopenhauer's pessimistic view that the world was as bad as it could be, and that, if it could grow in the least degree worse, it would be annihilated altogether, might be reversed and converted into an optimistic one: for it would be equally true to say that the world is as excellent as it is possible to make it with the given materials, and that a nearer approach to absolute perfection is inconceivable. The organic world teaches us that such is the case; each existing species shows the purpose of its being in every detail of its structure, and in its perfect adaptation to the conditions under which it lives. But it is only adapted so far as is actually necessary, only so far as to make it fittest to survive, and not a step further. The eye of

the frog is but an imperfect organ of vision as compared with the eye of the falcon, or that of man, but it is perfect enough to enable it to see the crawling fly or the writhing worm: it suffices for the needs of the species. Even the eye of the falcon is not absolutely perfect as an organ of vision from a purely optical point of view, but it serves to enable the bird to distinguish its prey with certainty from a great height: such a pitch of perfection is all that is essential for the life of the species, and all possibility of higher development of the eye, by means of natural selection, is therefore precluded. The object of all evolution, viz. the survival of the fittest, is not, however, always and only attained by the ever-improving, progressive development of the organism as a whole, or of particular organs: new possessions are not invariably added to the old, but the latter are often rendered superfluous in the course of time and taken away. Nor does this happen in an ideally perfect way, suddenly, as if by magic, but slowly, in accordance with existing laws, so that the process remains uncompleted through long ages. But ultimately the organ which is no longer essential to life is done away with altogether, and the balance between the structure of the body and its functions is restored, so that, in this sense also, retrogression may in truth be said to be a part of progress.