Development and Embryology.

This is one of the most important subjects in the whole round of natural history. The metamorphoses of insects, with which every one is familiar, are generally effected abruptly by a few stages; but the transformations are in reality numerous and gradual, though concealed. A certain ephemerous insect (Chlöeon) during its development, moults, as shown by Sir J. Lubbock, above twenty times, and each time undergoes a certain amount of change; and in this case we see the act of metamorphosis performed in a primary and gradual manner. Many insects, and especially certain crustaceans, show us what wonderful changes of structure can be effected during development. Such changes, however, reach their acme in the so- called alternate generations of some of the lower animals. It is, for instance, an astonishing fact that a delicate branching coralline, studded with polypi, and attached to a submarine rock, should produce, first by budding and then by transverse division, a host of huge floating jelly- fishes; and that these should produce eggs, from which are hatched swimming animalcules, which attach themselves to rocks and become developed into branching corallines; and so on in an endless cycle. The belief in the essential identity of the process of alternate generation and of ordinary metamorphosis has been greatly strengthened by Wagner's discovery of the larva or maggot of a fly, namely the Cecidomyia, producing asexually other larvæ, and these others, which finally are developed into mature males and females, propagating their kind in the ordinary manner by eggs.

It may be worth notice that when Wagner's remarkable discovery was first announced, I was asked how was it possible to account for the larvæ of this fly having acquired the power of a sexual reproduction. As long as the case remained unique no answer could be given. But already Grimm has shown that another fly, a Chironomus, reproduces itself in nearly the same manner, and he believes that this occurs frequently in the order. It is the pupa, and not the larva, of the Chironomus which has this power; and Grimm further shows that this case, to a certain extent, "unites that of the Cecidomyia with the parthenogenesis of the Coccidæ;" — the term parthenogenesis implying that the mature females of the Coccidæ are capable of producing fertile eggs without the concourse of the male. Certain animals belonging to several classes are now known to have the power of ordinary reproduction at an unusually early age; and we have only to accelerate parthenogenetic reproduction by gradual steps to an earlier and earlier age — Chironomus showing us an almost exactly intermediate stage, viz., that of the pupa — and we can perhaps account for the marvellous case of the Cecidomyia.

It has already been stated that various parts in the same individual, which are exactly alike during an early embryonic period, become widely different and serve for widely different purposes in the adult state. So again it has been shown that generally the embryos of the most distinct species belonging to the same class are closely similar, but become, when fully developed, widely dissimilar. A better proof of this latter fact cannot be given than the statement by Von Baer that "the embryos of mammalia, of birds, lizards and snakes, probably also of chelonia, are in the earliest states exceedingly like one another, both as a whole and in the mode of development of their parts; so much so, in fact, that we can often distinguish the embryos only by their size. In my possession are two little embryos in spirit, whose names I have omitted to attach, and at present I am quite unable to say to what class they belong. They may be lizards or small birds, or very young mammalia, so complete is the similarity in the mode of formation of the head and trunk in these animals. The extremities, however, are still absent in these embryos. But even if they had existed in the earliest stage of their development we should learn nothing, for the feet of lizards and mammals, the wings and feet of birds, no less than the

hands and feet of man, all arise from the same fundamental form." The larvæ of most crustaceans, at corresponding stages of development, closely resemble each other, however different the adults may become; and so it is with very many other animals. A trace of the law of embryonic resemblance occasionally lasts till a rather late age: thus birds of the same genus, and of allied genera, often resemble each other in their immature plumage; as we see in the spotted feathers in the young of the thrush group. In the cat tribe, most of the species when adult are striped or spotted in lines; and stripes or spots can be plainly distinguished in the whelp of the lion and the puma. We occasionally, though rarely, see something of the same kind in plants; thus the first leaves of the ulex or furze, and the first leaves of the phyllodineous acacias, are pinnate or divided like the ordinary leaves of the leguminosæ.

The points of structure, in which the embryos of widely different animals within the same class resemble each other, often have no direct relation to their conditions of existence. We cannot, for instance, suppose that in the embryos of the vertebrata the peculiar loop-like courses of the arteries near the branchial slits are related to similar conditions — in the young mammal which is nourished in the womb of its mother, in the egg of the bird which is hatched in a nest, and in the spawn of a frog under water. We have no more reason to believe in such a relation than we have to believe that the similar bones in the hand of a man, wing of a bat, and fin of a porpoise, are related to similar conditions of life. No one supposes that the stripes on the whelp of a lion, or the spots on the young blackbird, are of any use to these animals.

The case, however, is different when an animal, during any part of its embryonic career, is active, and has to provide for itself. The period of activity may come on earlier or later in life; but whenever it comes on, the adaptation of the larva to its conditions of life is just as perfect and as beautiful as in the adult animal. In how important a manner this has acted, has recently been well shown by Sir J. Lubbock in his remarks on the close similarity of the larvæ of some insects belonging to very different orders, and on the dissimilarity of the larvæ of other insects within the same order, according to their habits of life. Owing to such adaptations the similarity of the larvæ of allied animals is sometimes greatly obscured; especially when there is a division of labour during the different stages of development, as when the same larva has during one stage to search for food, and during another stage has to search for a place of attachment. Cases can even be given of the larvæ of allied species, or groups of species, differing more from each other than do the adults. In most cases, however, the larvæ, though active, still obey, more or less closely, the law of common embryonic resemblance. Cirripedes afford a good instance of this: even the illustrious Cuvier did not perceive that a barnacle was a crustacean: but a glance at the larva shows this in an unmistakable manner. So again the two main divisions of cirripedes, the pedunculated and sessile, though differing widely in external appearance, have larvæ in all their stages barely distinguishable.

The embryo in the course of development generally rises in organisation. I use this expression, though I am aware that it is hardly possible to define clearly what is meant by organisation being higher or lower. But no one probably will dispute that the butterfly is higher than the caterpillar. In some cases, however, the mature animal must be considered as lower in the scale than the larva, as with certain parasitic crustaceans. To refer once again to cirripedes: the larvæ in the first stage have three pairs of locomotive organs, a simple single eye, and a probosciformed mouth, with which they feed largely, for they increase much in size. In the second stage, answering to the chrysalis stage of butterflies, they have six pairs of beautifully constructed natatory legs, a pair of magnificent compound eyes, and extremely complex antennae; but they have a closed and imperfect mouth, and cannot feed: their function at this stage is, to search out by their well-developed organs of sense, and to reach by their active powers of swimming, a proper place on which to become attached and to undergo their final

metamorphosis. When this is completed they are fixed for life: their legs are now converted into prehensile organs; they again obtain a well-constructed mouth; but they have no antennæ, and their two eyes are now reconverted into a minute, single, simple eye-spot. In this last and complete state, cirripedes may be considered as either more highly or more lowly organised than they were in the larval condition. But in some genera the larvæ become developed into hermaphrodites having the ordinary structure, or into what I have called complemental males; and in the latter the development has assuredly been retrograde; for the male is a mere sack, which lives for a short time and is destitute of mouth, stomach, and every other organ of importance, excepting those for reproduction.

We are so much accustomed to see a difference in structure between the embryo and the adult, that we are tempted to look at this difference as in some necessary manner contingent on growth. But there is no reason why, for instance, the wing of a bat, or the fin of a porpoise, should not have been sketched out with all their parts in proper proportion, as soon as any part became visible. In some whole groups of animals and in certain members of other groups this is the case, and the embryo does not at any period differ widely from the adult: thus Owen has remarked in regard to cuttle-fish, "there is no metamorphosis; the cephalopodic character is manifested long before the parts of the embryo are completed." Land-shells and fresh-water crustaceans are born having their proper forms, while the marine members of the same two great classes pass through considerable and often great changes during their development. Spiders, again, barely undergo any metamorphosis. The larvæ of most insects pass through a worm-like stage, whether they are active and adapted to diversified habits, or are inactive from being placed in the midst of proper nutriment, or from being fed by their parents; but in some few cases, as in that of Aphis, if we look to the admirable drawings of the development of this insect, by Professor Huxley, we see hardly any trace of the vermiform stage.

Sometimes it is only the earlier developmental stages which fail. Thus, Fritz Müller has made the remarkable discovery that certain shrimp-like crustaceans (allied to Penœus) first appear under the simple nauplius- form, and after passing through two or more zoea-stages, and then through the mysis-stage, finally acquire their mature structure: now in the whole great malacostracan order, to which these crustaceans belong, no other member is as yet known to be first developed under the nauplius-form, though many appear as zoeas; nevertheless Müller assigns reasons for his belief, that if there had been no suppression of development, all these crustaceans would have appeared as nauplii.

How, then, can we explain these several facts in embryology,— namely, the very general, though not universal, difference in structure between the embryo and the adult;— the various parts in the same individual embryo, which ultimately become very unlike, and serve for diverse purposes, being at an early period of growth alike;— the common, but not invariable, resemblance between the embryos or larvæ of the most distinct species in the same class; the embryo often retaining, while within the egg or womb, structures which are of no service to it, either at that or at a later period of life; on the other hand, larvæ which have to provide for their own wants, being perfectly adapted to the surrounding conditions;— and lastly, the fact of certain larvæ standing higher in the scale of organisation than the mature animal into which they are developed? I believe that all these facts can be explained as follows.

It is commonly assumed, perhaps from monstrosities affecting the embryo at a very early period, that slight variations or individual differences necessarily appear at an equally early period. We have little evidence on this head, but what we have certainly points the other way; for it is notorious that breeders of cattle, horses and various fancy animals, cannot positively tell, until some time after birth, what will be the merits and demerits of their young animals. We see this plainly in our own children; we cannot tell whether a child will be tall or short, or what its precise features will be. The question is not, at what

period of life any variation may have been caused, but at what period the effects are displayed. The cause may have acted, and I believe often has acted, on one or both parents before the act of generation. It deserves notice that it is of no importance to a very young animal, as long as it is nourished and protected by its parent, whether most of its characters are acquired a little earlier or later in life. It would not signify, for instance, to a bird which obtained its food by having a much-curved beak whether or not while young it possessed a beak of this shape, as long as it was fed by its parents.

I have stated in the first chapter, that at whatever age any variation first appears in the parent, it tends to reappear at a corresponding age in the offspring. Certain variations can only appear at corresponding ages; for instance, peculiarities in the caterpillar, cocoon, or imago states of the silk-moth; or, again, in the full-grown horns of cattle. But variations which, for all that we can see might have appeared either earlier or later in life, likewise tend to reappear at a corresponding age in the offspring and parent. I am far from meaning that this is invariably the case, and I could give several exceptional cases of variations (taking the word in the largest sense) which have supervened at an earlier age in the child than in the parent.

These two principles, namely, that slight variations generally appear at a not very early period of life, and are inherited at a corresponding not early period, explain, as I believe, all the above specified leading facts in embryology. But first let us look to a few analogous cases in our domestic varieties. Some authors who have written on Dogs maintain that the greyhound and bull-dog, though so different, are really closely allied varieties, descended from the same wild stock, hence I was curious to see how far their puppies differed from each other. I was told by breeders that they differed just as much as their parents, and this, judging by the eye, seemed almost to be the case; but on actually measuring the old dogs and their six-days-old puppies, I found that the puppies had not acquired nearly their full amount of proportional difference. So, again, I was told that the foals of cart and race-horses — breeds which have been almost wholly formed by selection under domestication — differed as much as the full-grown animals; but having had careful measurements made of the dams and of three-days-old colts of race and heavy cart-horses, I find that this is by no means the case.

As we have conclusive evidence that the breeds of the Pigeon are descended from a single wild species, I compared the young pigeons within twelve hours after being hatched. I carefully measured the proportions (but will not here give the details) of the beak, width of mouth, length of nostril and of eyelid, size of feet and length of leg, in the wild parent species, in pouters, fantails, runts, barbs, dragons, carriers, and tumblers. Now, some of these birds, when mature, differ in so extraordinary a manner in the length and form of beak, and in other characters, that they would certainly have been ranked as distinct genera if found in a state of nature. But when the nestling birds of these several breeds were placed in a row, though most of them could just be distinguished, the proportional differences in the above specified points were incomparably less than in the full-grown birds. Some characteristic points of difference — for instance, that of the width of mouth — could hardly be detected in the young. But there was one remarkable exception to this rule, for the young of the short-faced tumbler differed from the young of the wild rock-pigeon, and of the other breeds, in almost exactly the same proportions as in the adult stage.

These facts are explained by the above two principles. Fanciers select their dogs, horses, pigeons, &c., for breeding, when nearly grown up. They are indifferent whether the desired qualities are acquired earlier or later in life, if the full-grown animal possesses them. And the cases just given, more especially that of the pigeons, show that the characteristic differences which have been accumulated by

man's selection, and which give value to his breeds, do not generally appear at a very early period of life, and are inherited at a corresponding not early period. But the case of the short-faced tumbler, which when twelve hours old possessed its proper characters, proves that this is not the universal rule; for here the characteristic differences must either have appeared at an earlier period than usual, or, if not so, the differences must have been inherited, not at a corresponding, but at an earlier age.

Now, let us apply these two principles to species in a state of nature. Let us take a group of birds, descended from some ancient form and modified through natural selection for different habits. Then, from the many slight successive variations having supervened in the several species at a not early age, and having been inherited at a corresponding age, the young will have been but little modified, and they will still resemble each other much more closely than do the adults,— just as we have seen with the breeds of the pigeon. We may extend this view to widely distinct structures and to whole classes. The fore-limbs, for instance, which once served as legs to a remote progenitor, may have become, through a long course of modification, adapted in one descendant to act as hands, in another as paddles, in another as wings; but on the above two principles the fore-limbs will not have been much modified in the embryos of these several forms; although in each form the fore-limb will differ greatly in the adult state. Whatever influence long continued use or disuse may have had in modifying the limbs or other parts of any species, this will chiefly or solely have affected it when nearly mature, when it was compelled to use its full powers to gain its own living; and the effects thus produced will have been transmitted to the offspring at a corresponding nearly mature age. Thus the young will not be modified, or will be modified only in a slight degree, through the effects of the increased use or disuse of parts.

With some animals the successive variations may have supervened at a very early period of life, or the steps may have been inherited at an earlier age than that at which they first occurred. In either of these cases the young or embryo will closely resemble the mature parent-form, as we have seen with the short-faced tumbler. And this is the rule of development in certain whole groups, or in certain sub-groups alone, as with cuttle-fish, land-shells, fresh-water crustaceans, spiders, and some members of the great class of insects. With respect to the final cause of the young in such groups not passing through any metamorphosis, we can see that this would follow from the following contingencies: namely, from the young having to provide at a very early age for their own wants, and from their following the same habits of life with their parents; for in this case it would be indispensable for their existence that they should be modified in the same manner as their parents. Again, with respect to the singular fact that many terrestrial and fresh-water animals do not undergo any metamorphosis, while marine members of the same groups pass through various transformations, Fritz Müller has suggested that the process of slowly modifying and adapting an animal to live on the land or in fresh water, instead of in the sea, would be greatly simplified by its not passing through any larval stage; for it is not probable that places well adapted for both the larval and mature stages, under such new and greatly changed habits of life, would commonly be found unoccupied or ill-occupied by other organisms. In this case the gradual acquirement at an earlier and earlier age of the adult structure would be favoured by natural selection; and all traces of former metamorphoses would finally be lost.

If, on the other hand, it profited the young of an animal to follow habits of life slightly different from those of the parent-form, and consequently to be constructed on a slightly different plan, or if it profited a larva already different from its parent to change still further, then, on the principle of inheritance at corresponding ages, the young or the larvæ might be rendered by natural selection more and more different from their parents to any conceivable extent. Differences in the larva might, also, become correlated with successive stages of its development; so that the larva, in the first stage, might

come to differ greatly from the larva in the second stage, as is the case with many animals. The adult might also become fitted for sites or habits, in which organs of locomotion or of the senses, &c., would be useless; and in this case the metamorphosis would be retrograde.

From the remarks just made we can see how by changes of structure in the young, in conformity with changed habits of life, together with inheritance at corresponding ages, animals might come to pass through stages of development, perfectly distinct from the primordial condition of their adult progenitors. Most of our best authorities are now convinced that the various larval and pupal stages of insects have thus been acquired through adaptation, and not through inheritance from some ancient form. The curious case of Sitaris — a beetle which passes through certain unusual stages of development — will illustrate how this might occur. The first larval form is described by M. Fabre, as an active, minute insect, furnished with six legs, two long antennæ, and four eyes. These larvæ are hatched in the nests of bees; and when the male bees emerge from their burrows, in the spring, which they do before the females, the larvæ spring on them, and afterwards crawl on to the females while paired with the males. As soon as the female bee deposits her eggs on the surface of the honey stored in the cells, the larvæ of the Sitaris leap on the eggs and devour them. Afterwards they undergo a complete change; their eyes disappear; their legs and antennæ become rudimentary, and they feed on honey; so that they now more closely resemble the ordinary larvæ of insects; ultimately they undergo a further transformation, and finally emerge as the perfect beetle. Now, if an insect, undergoing transformations like those of the Sitaris, were to become the progenitor of a whole new class of insects, the course of development of the new class would be widely different from that of our existing insects; and the first larval stage certainly would not represent the former condition of any adult and ancient form.

On the other hand it is highly probable that with many animals the embryonic or larval stages show us, more or less completely, the condition of the progenitor of the whole group in its adult state. In the great class of the Crustacea, forms wonderfully distinct from each other, namely, suctorial parasites, cirripedes, entomostraca, and even the malacostraca, appear at first as larvæ under the nauplius-form; and as these larvæ live and feed in the open sea, and are not adapted for any peculiar habits of life, and from other reasons assigned by Fritz Müller, it is probable that at some very remote period an independent adult animal, resembling the Nauplius, existed, and subsequently produced, along several divergent lines of descent, the above-named great Crustacean groups. So again, it is probable, from what we know of the embryos of mammals, birds, fishes and reptiles, that these animals are the modified descendants of some ancient progenitor, which was furnished in its adult state with branchiæ, a swim- bladder, four fin-like limbs, and a long tail, all fitted for an aquatic life.

As all the organic beings, extinct and recent, which have ever lived, can be arranged within a few great classes; and as all within each class have, according to our theory, been connected together by fine gradations, the best, and, if our collections were nearly perfect, the only possible arrangement, would be genealogical; descent being the hidden bond of connexion which naturalists have been seeking under the term of the Natural System. On this view we can understand how it is that, in the eyes of most naturalists, the structure of the embryo is even more important for classification than that of the adult. In two or more groups of animals, however much they may differ from each other in structure and habits in their adult condition, if they pass through closely similar embryonic stages, we may feel assured that they are all descended from one parent- form, and are therefore closely related. Thus, community in embryonic structure reveals community of descent; but dissimilarity in embryonic development does not prove discommunity of descent, for in one of two groups the developmental stages may have been suppressed, or may have been so greatly modified through adaptation to new

habits of life as to be no longer recognisable. Even in groups, in which the adults have been modified to an extreme degree, community of origin is often revealed by the structure of the larvae; we have seen, for instance, that cirripedes, though externally so like shell-fish, are at once known by their larvæ to belong to the great class of crustaceans. As the embryo often shows us more or less plainly the structure of the less modified and ancient progenitor of the group, we can see why ancient and extinct forms so often resemble in their adult state the embryos of existing species of the same class. Agassiz believes this to be a universal law of nature; and we may hope hereafter to see the law proved true. It can, however, be proved true only in those cases in which the ancient state of the progenitor of the group has not been wholly obliterated, either by successive variations having supervened at a very early period of growth, or by such variations having been inherited at an earlier age than that at which they first appeared. It should also be borne in mind, that the law may be true, but yet, owing to the geological record not extending far enough back in time, may remain for a long period, or for ever, incapable of demonstration. The law will not strictly hold good in those cases in which an ancient form became adapted in its larval state to some special line of life, and transmitted the same larval state to a whole group of descendants; for such larval state will not resemble any still more ancient form in its adult state.

Thus, as it seems to me, the leading facts in embryology, which are second to none in importance, are explained on the principle of variations in the many descendants from some one ancient progenitor, having appeared at a not very early period of life, and having been inherited at a corresponding period. Embryology rises greatly in interest, when we look at the embryo as a picture, more or less obscured, of the progenitor, either in its adult or larval state, of all the members of the same great class.

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