# CHAPTER XI.

## ON THE PROGRESS OF EVOLUTION.

FROM this scarcely unavoidable but unsatisfactory side-glance upon the old school, which looks down with so great an air of superiority upon Darwin's "intellectual dream" and the "giddy enthusiasm" of its friends, I turn to the more congenial task of considering the developmental history of the Crustacea from the point of view of the Darwinian theory.

Darwin himself, in the thirteenth chapter of his book, has already discussed the conclusions derived from his hypotheses in the domain of developmental history. For a more detailed application of them, however, it is necessary in the first place to trace these general conclusions a little further than he has there done.

The changes by which young animals depart from their parents, and the gradual accumulation of which causes the production of new species, genera, and families, may occur at an earlier or later period of life, —in the young state, or at the period of sexual maturity. For the latter is by no means always, as in the Insecta, a period of repose; most other animals even then continue to grow and to undergo changes.

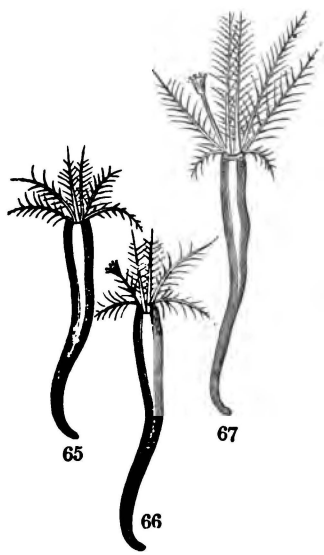
(See above, the remarks on the males of the Amphipoda.) Some variations, indeed, from their very nature, can only occur when the young animal has attained the adult stage of development. Thus the Sea Caterpillars (*Polynoë*) at first possess only a few body-segments, which, during development, gradually increase to a number which is different in different species, but constant in the same species; now before a young animal could exceed the number of segments of its parents, it must of course have attained that number. We may assume a similar supplementary progress wherever the deviation of the descendants consists in an addition of new segments and limbs.

*Descendants therefore reach a new goal, either by deviating sooner or later whilst still on the way towards the form of their parents, or by passing along this course without deviation, but then, instead of standing still, advance still farther.*

The former mode will have had a predominant action where the posterity of common ancestors constitutes a group of forms standing upon the same level in essential features, as the whole of the Amphipoda, Crabs, or Birds. On the other hand we are led to the assumption of the second mode of progress, when we seek to deduce from a common original form, animals some of which agree with young states of others.

In the former case the developmental history of the descendants can only agree with that of their ancestors up to a certain point at which their courses separate,—as to their structure in the adult state it will teach us

nothing. *In the second case the entire development of the progenitors is also passed through by the descendants, and, therefore, so far as the production of a species depends upon this second mode of progress, the historical development of the species will be mirrored in its developmental history.* In the short period of a few weeks or months, the changing forms of the embryo and larvæ will pass before us, a more or less complete and more or less true picture of the transformations through which the species, in the course of untold thousands of years, has struggled up to its present state.



Figs. 65, 66, 67.[1]

One of the simplest examples is furnished by the development of the Tubicolar Annelids; but from its very simplicity it appears well adapted to open the eyes of many who, perhaps, would rather

[1] Figs. 65–67. Young Tubicolar worms, magnified with the simple lens about 6 diam.: 65.[a] without operculum, *Protula*-stage; 66. with a barbate opercular peduncle, *Filograna*-stage; 67. with a naked opercular peduncle, *Serpula*-stage.

[a] Fig. 65 is drawn from memory, as the little animals, which I at first took for young *Protulæ*, only attracted my attention when I remarked the appearance of the operculum, which induced me to draw them.

not see, and it may therefore find a place here. Three years ago I found on the walls of one of my glasses some small worm-tubes (fig. 65), the inhabitants of which bore three pairs of barbate branchial filaments, and had no operculum. According to this we should have been obliged to refer them to the genus *Protula*. A few days afterwards one of the branchial filaments had become thickened at the extremity into a clavate operculum (fig. 66), when the animals reminded me, by the barbate opercular peduncle, of the genus *Filograna*, only that the latter possesses two opercula. In three days more, during which a new pair of branchial filaments had sprouted forth, the opercular peduncle had lost its lateral filaments (fig. 67), and the worms had become *Serpulæ*. Here the supposition at once presents itself that the primitive tubicolar worm was a *Protula*,—that some of its descendants, which had already become developed into perfect *Protulæ*, subsequently improved themselves by the formation of an operculum which might protect their tubes from inimical intruders,—and that subsequent descendants of these latter finally lost the lateral filaments of the opercular peduncle, which they, like their ancestors, had developed.

What say the schools to this case? Whence and for what purpose, if the *Serpulæ* were produced or created as ready-formed species, these lateral filaments of the opercular peduncle? To allow them to sprout forth merely for the sake of an invariable plan of structure, even when they must be immediately re-

tracted again as superfluous, would certainly be an evidence rather of childish trifling or dictatorial pedantry, than of infinite wisdom. But no, I am mistaken; from the beginning of all things the Creator knew, that one day the inquisitive children of men would grope about after analogies and homologies, and that Christian naturalists would busy themselves with thinking out his Creative ideas; at any rate, in order to facilitate the discernment by the former that the opercular peduncle of the *Serpulæ* is homologous with a branchial filament, He allowed it to make a *détour* in its development, and pass through the form of a barbate branchial filament.

*The historical record preserved in developmental history is gradually* EFFACED *as the development strikes into a constantly straighter course from the egg to the perfect animal, and it is frequently* SOPHISTICATED *by the struggle for existence which the free-living larvæ have to undergo.*

Thus as the law of inheritance is by no means strict, as it gives room for individual variations with regard to the form of the parents, this is also the case with the succession in time of the developmental processes. Every father of a family who has taken notice of such matters, is well aware that even in children of the same parents, the teeth, for example, are not cut or changed, either at the same age, or in the same order. Now in general it will be useful to an animal to obtain as early as possible those advantages by which it sustains itself in the struggle for existence. A precocious appearance of peculiarities originally acquired at a later

period will generally be advantageous, and their retarded appearance disadvantageous; the former, when it appears accidentally, will be preserved by natural selection. It is the same with every change which gives to the larval stages, rendered multifarious by crossed and oblique characters, a more straightforward direction, simplifies and abridges the process of development, and forces it back to an earlier period of life, and finally into the life of the egg.

As this conversion of a development passing through different young states into a more direct one, is not the consequence of a mysterious inherent impulse, but dependent upon advances accidentally presenting themselves, it may take place in the most nearly allied animals in the most various ways, and require very different periods of time for its completion. There is one thing, however, that must not be overlooked here. The historical development of a species can hardly ever have taken place in a continuously uniform flow; periods of rest will have alternated with periods of rapid progress. But forms, which in periods of rapid progress were severed from others after a short duration, must have impressed themselves less deeply upon the developmental history of their descendants, than those which repeated themselves unchanged, through a long series of successive generations in periods of rest. These more fixed forms, less inclined to variation, will present a more tenacious resistance in the transition to direct development, and will maintain themselves in a more uniform manner and to the last, however

different may be the course of this process in other respects.

In general, as already stated, it will be advantageous to the young to commence the struggle for existence in the form of their parents and furnished with all their advantages—in general, but not without exceptions. It is perfectly clear that a brood capable of locomotion is almost indispensable to attached animals, and that the larvæ of sluggish Mollusca, or of worms burrowing in the ground, &c., by swarming briskly through the sea perform essential services by dispersing the species over wider spaces. In other cases a metamorphosis is rendered indispensable by the circumstance that a division of labour has been set up between the various periods of life; for example, that the larvæ have exclusively taken upon themselves the business of nourishment. A further circumstance to be taken into consideration is the size of the eggs,—a simpler structure may be produced with less material than a more compound one,—the more imperfect the larva, the smaller may the egg be, and the larger is the number of these that the mother can furnish with the same expenditure of material. As a rule, I believe indeed, this advantage of a more numerous brood will not by any means outweigh that of a more perfect brood, but it will do so in those cases in which the chief difficulty of the young animals consists in finding a suitable place for their development, and in which, therefore, it is of importance to disperse the greatest possible number of germs, as in many parasites.

As the conversion of the original development with metamorphosis into direct development is here under discussion, this may be the proper place to say a word as to the already indicated absence of metamorphosis in fresh-water and terrestrial animals the marine allies of which still undergo a transformation. This circumstance seems to be explicable in two ways. Either species without a metamorphosis migrated especially into the fresh waters, or the metamorphosis was more rapidly got rid of in the emigrants than in their fellows remaining in the sea.

Animals without a metamorphosis would naturally transfer themselves more easily to a new residence, as they had only themselves and not at the same time multifarious young forms to adapt to the new conditions. But in the case of animals with a metamorphosis, the mortality among the larvæ, always considerable, must have become still greater under new than under accustomed conditions, every step towards the simplification of the process of development must therefore have given them a still greater preponderance over their fellows, and the effacing of the metamorphosis must have gone on more rapidly. What has taken place in each individual case, whether the species has immigrated after it had lost the metamorphosis, or lost the metamorphosis after its immigration, will not always be easy to decide. When there are marine allies without, or with only a slight metamorphosis, like the Lobster as the cousin of the Cray-fish, we may take up the former supposition; when allies with a

metamorphosis still live upon the land or in fresh water, as in the case of *Gecarcinus*, we may adopt the latter.

That besides this gradual extinction of the primitive history, a *falsification* of the record preserved in the developmental history takes place by means of the struggle for existence which the free-living young states have to undergo, requires no further exposition. For it is perfectly evident that the struggle for existence and natural selection combined with this, must act in the same way, in change and development, upon larvæ which have to provide for themselves, as upon adult animals. The changes of the larvæ, independent of the progress of the adult animal, will become the more considerable, the longer the duration of the life of the larva in comparison to that of the adult animal, the greater the difference in their mode of life, and the more sharply marked the division of labour between the different stages of development. These processes have to a certain extent an action opposed to the gradual extinction of the primitive history; they increase the differences between the individual stages of development, and it will be easily seen how even a straightforward course of development may be again converted by them into a development with metamorphosis. By this means many, and it seems to me valid reasons may be brought up in favour of the opinion that the most ancient Insects approached more nearly to the existing Orthoptera, and perhaps to the wingless Blattidæ, than to any other order, and that the "com-

plete metamorphosis" of the Beetles, Lepidoptera, &c., is of later origin. There were, I believe, perfect Insects before larvæ and pupæ; but, on the contrary, Nauplii and Zoëæ far earlier than perfect Prawns. In contradistinction to the *inherited* metamorphosis of the Prawns, we may call that of the Coleoptera, Lepidoptera, &c., an *acquired* metamorphosis.[2]

[2] I will here briefly give my reasons for the opinion that the so-called "complete metamorphosis" of Insects, in which these animals quit the egg as grubs or caterpillars, and afterwards become quiescent pupæ incapable of feeding, was not inherited from the primitive ancestor of all Insects, but acquired at a later period.

The order Orthoptera, including the Pseudoneuroptera (*Ephemera*, *Libellula*, &c.) appears to approach nearest to the primitive form of Insects. In favour of this view we have:—

1. The structure of their buccal organs, especially the formation of the labium, "which retains, either perfectly or approximately, the original form of a second pair of maxillæ" (Gerstäcker).

2. The segmentation of the abdomen; "like the labium, the abdomen also very generally retains its original segmentation, which is shown in the development of eleven segments" (Gerstäcker). The Orthoptera with eleven segments in the abdomen, agree perfectly in the number of their body-segments with the Prawn-larva represented in fig. 33, or indeed, with the higher Crustacea (Podophthalma and Edriophthalma) in general, in which the historically youngest last thoracic segment (see p. 123), which is sometimes late-developed, or destitute of appendages, or even deficient, is still wanting.

3. That, as in the Crustacea, the sexual orifice and anus are placed upon different segments; "whilst the former is situated in the ninth segment, the latter occurs in the eleventh" (Gerstäcker).

4. Their palæontological occurrence; "in a fossil state the Orthoptera make their appearance the earliest of all Insects, namely as early as the Carboniferous formation, in which they exceed all others in number" (Gerstäcker).

5. The absence of uniformity of habit at the present day in an order so small when compared with the Coleoptera, Hymenoptera, &c. For this also is usually a phenomenon characteristic of very ancient groups of forms which have already overstepped the climax of their development, and is explicable by extinction in mass. A Beetle or a Butterfly is to be recognised as such at the first glance, but only a thorough

Which of the different modes of development at present occurring in a class of animals may claim to be

investigation can demonstrate the mutual relationships of *Termes*, *Blatta*, *Mantis*, *Forficula*, *Ephemera*, *Libellula*, &c. I may refer to a corresponding remarkable example from the vegetable world: amongst Ferns the genera *Aneimia*, *Schizæa* and *Lygodium*, belonging to the group *Schizæaceæ* which is very poor in species, differ much more from each other than any two forms of the group *Polypodiaceæ* which numbers its thousands of species.

If, from all this, it seems right to regard the Orthoptera as the order of Insects approaching most nearly to the common primitive form, we must also expect that their mode of development will agree better with that of the primitive form, than, for example, that of the Lepidoptera, in the same way that some of the Prawns (*Penæus*) approaching most closely the primitive form of the Decapoda, have most truly preserved their original mode of development. Now, the majority of the Orthoptera quit the egg in a form which is distinguished from that of the adult Insect almost solely by the want of wings; these larvæ then soon acquire rudiments of wings, which appear more strongly developed after every moult. Even this perfectly gradual transition from the youngest larva to the sexually mature Insect, preserves in a far higher degree the picture of an original mode of development, than does the so-called complete metamorphosis of the Coleoptera, Lepidoptera, or Diptera, with its abruptly separated larva-, pupa- and imago-states.

The most ancient Insects would probably have most resembled these wingless larvæ of the existing Orthoptera. The circumstance that there are still numerous wingless species among the Orthoptera, and that some of these (*Blattidæ*) are so like certain Crustacea (Isopods) in habit that both are indicated by the same name ("*Baratta*") by the people in this country, can scarcely be regarded as of any importance.

The contrary supposition that the oldest Insects possessed a "complete metamorphosis," and that the "incomplete metamorphosis" of the Orthoptera and Hemiptera is only of later origin, is met by serious difficulties. If all the classes of Arthropoda (Crustacea, Insecta, Myriopoda and Arachnida) are indeed all branches of a common stem (and of this there can scarcely be a doubt), it is evident that the water-inhabiting and water-breathing Crustacea must be regarded as the original stem from which the other terrestrial classes, with their tracheal respiration, have branched off. But nowhere among the Crustacea is there a mode of development comparable to the "complete metamorphosis" of the Insecta, nowhere among the young or adult

that approaching most nearly to the original one, is easy to judge from the above statements.

*The primitive history of a species will be preserved in its developmental history the more perfectly, the longer the series of young states through which it passes by uniform steps; and the more truly, the less the mode of life of the young departs from that of the adults, and the less the peculiarities of the individual young states can be conceived as transferred back from later ones in previous periods of life, or as independently acquired.*

Let us apply this to the Crustacea.

Crustacea are there forms which might resemble the maggots of the Diptera or Hymenoptera, the larvæ of the Coleoptera, or the caterpillars of the Lepidoptera, still less any bearing even a distant resemblance to the quiescent pupæ of these animals. The pupæ, indeed, cannot at all be regarded as members of an original developmental series, the individual stages of which represent permanent ancestral states, for an animal like the mouthless and footless pupa of the Silkworm, enclosed by a thick cocoon, can never have formed the final, sexually mature state of an Arthropod.

In the development of the Insecta we never see new segments added to those already present in the youngest larvæ, but we do see segments which were distinct in the larva afterwards become fused together or disappear. Considering the parallelism which prevails throughout organic nature between palæontological and embryonic development, it is therefore improbable that the oldest Insects should have possessed fewer segments than some of their descendants. But the larvæ of the Coleoptera, Lepidoptera, &c., never have more than nine abdominal segments, it is therefore not probable that they represent the original young form of the oldest Insects, and that the Orthoptera, with an abdomen of eleven segments, should have been subsequently developed from them.

Taking into consideration on the one hand these difficulties, and on the other the arguments which indicate the Orthoptera as the order most nearly approaching the primitive form, it is my opinion that the "incomplete metamorphosis" of the Orthoptera is the primitive one, *inherited* from the original parents of all Insects, and the "complete metamorphosis" of the Coleoptera, Diptera, &c., a subsequently *acquired* one.