CHAPTER XII.

PROGRESS OF EVOLUTION IN CRUSTACEA.

ACCORDING to all the characters established in the last paragraph, the Prawn that we traced from the Nauplius through states analogous to Zoëa and Mysis to the form of a Macrurous Crustacean appears at present to be the animal, which in the section of the higher Crustacea (Malacostraca) furnishes the truest and most complete indications of its primitive history. That it is the most complete is at once evident. That it is the truest must be assumed, in the first place, because the mode of life of the various ages is less different than in the majority of the other Podophthalma; for from the Nauplius to the young Prawn they were found swimming freely in the sea, whilst Crabs, Porcellana, the Tatuira, Squilla, and many Macrura, when adult usually reside under stones, in the clefts of rocks, holes in the earth, subterranean galleries, sand, &c., not to mention other deviations in habits such as are presented by the Hermit Crabs, Pinnotheres, &c.,—and secondly and especially because the peculiarities which distinguish the Zoëa of this species particularly from other Zoëæ (the employment of the anterior limbs for swimming, the furcate tail, the simple heart, the deficiency of the paired eyes and abdomen at first, &c.) are neither to be deduced from a retro-transfer of late-acquired advantages to this early period of life, nor to be regarded at all as advantages over other Zoëæ which the larva might have acquired in the struggle for existence.

A similar development must have been once passed through by the primitive ancestor of all Malacostraca, probably differing from that of our Prawn, especially in the circumstance that it would go on more uniformly without the sudden change of form and mode of locomotion produced in the latter by the simultaneous sprouting forth and entering into action in the Nauplius of four and in the Zoëa of five pairs of limbs. It is to be supposed that, not only originally but even still, in the larvæ of the first Malacostraca, the new body-segments and pairs of limbs are formed singly,-first of all the segments of the fore-body, then those of the abdomen. and finally those of the middle-body,—and, moreover, that in each region of the body the anterior segments were formed earlier than the posterior ones, and therefore last of all the hindermost segment of the middlebody. Of this original mode more or less distinct traces still remain, even in species in which, in other respects, the course of development of their ancestors is already nearly effaced. Thus the abdominal feet of the Prawnlarva represented in fig. 33, are formed singly from before backwards, and after these the last feet of the middle-body; thus, in Palinurus, the last two pairs of feet of the middle-body are formed later than the rest; thus in the young larvæ of the Stomapoda the last

three abdominal segments are destitute of limbs, which are still wanting on the last of them in older larvæ; and thus, in the Isopoda, the historically newest pair of feet is produced later than all the rest. In the Copepoda this formation of new segments and limbs, gradually advancing from before backwards, is more perfectly preserved than in any of the higher Crustacea.

The original development of the Malacostraca starting from the Nauplius, or the lowest free-living grade with which we are acquainted in the class of Crustacea, is now-a-days nearly effaced in the majority of them. That this extinction has actually taken place in the way already deduced as a direct consequence from Darwin's theory, will be the more easily demonstrated, the more this process is still included in the course of life, and the less completely it is already worn out. We may hope to obtain the most striking examples in the still unknown developmental history of the various Schizopoda, Peneïdæ, and, indeed, of the Macrura in general. At present the multifarious Zoëa-forms appear to be

¹ It is well known that, in many cases, even in adult animals the last segment of the middle-body, or some of its last segments, either want their limbs or are themselves deficient (Entoniscus Porcellane 3, Leucifer, &c.). This might be due to the animals having separated from the common stem before these limbs were formed at all. But in those cases with which I am best acquainted, it seems to me more probable that the limbs have been subsequently lost again. That these particular limbs and segments are more easily lost than others is explained by the circumstance that, as the youngest, they have been less firmly fixed by long-continued inheritance. ("Mr. Dana believes, that in ordinary Crustaceans, the abortion of the segments with their appendages almost always takes place at the posterior end of the cephalothorax."—Darwin, Balanidæ, p. 111.)

particularly instructive. Almost all the peculiarities by which they depart from the primitive form of the Zoëa of Penëus (figs. 29, 30, 32), may in fact be conceived as transferred back from a later period into this early period of life. This is the case with the large compound eyes,—with the structure of the heart,—with the raptorial feet in Squilla,—and with the powerful, muscular, straightly-extended abdomen in Palæmon, Alpheus, Hippolyte, and the Hermit Crabs. (In the latter, indeed, the abdomen of the adult animal is a shapeless sac filled with the liver and generative organs, but it is still tolerably powerful in the Glaucothoë-stage, and was certainly still more powerful when this stage was still the permanent form of the animal.) It is also the case with the abdomen of the Zoëæ of the Crabs, the Porcellanæ, and the Tatuira, which is still powerful, although usually bent under the breast; the two last swim tolerably by means of the abdomen, even when adult, as do the true Crabs in the young state known as Megalops. It is the case, lastly, with the conversion of the two anterior pairs of limbs into antennæ. second pair of antennæ, which, in the various Zoëæ always remains a step behind that of the adult animal, is particularly remarkable. In the Crabs the "scale" is entirely wanting; their Zoëæ have it indicated in the form of a moveable appendage, which is often exceedingly minute. In the Hermit Crabs a similar, usually moveable, spiniform process occurs as the remains of the scale; their Zoëæ have a well-developed but inarticulate scale. A precisely similar scale is possessed

by the adult Prawns, in the Zoëæ of which it exists still in a jointed form, like the outer branch of the second pair of feet of the Nauplius or *Penēus*-Zoëa.

The long, spiniform processes on the carapace of the Zoëæ of the Crabs and Porcellanæ are not to be explained in this way, but their advantage to the larvæ is evident. Thus, for example, if the body of the Zoëa of Porcellana stellicola (fig. 24), without the processes of the carapace and without the abdomen, which however is not rigidly extensible, is scarcely half a line in length, whilst with the processes it is four lines long, a mouth of eight times the width is necessary in order to swallow the little animal when thus armed. Consequently these processes of the carapace may be regarded as acquired by the Zoëa itself in the struggle for existence.

The formation of new limbs beneath the skin of the larvæ is also to be referred to an earlier occurrence of processes which originally took place at a later period. The original course must have been that they sprouted forth in a free form upon the ventral surface of the larva in the next stage after the change of skin; whilst now they are developed before the change of skin, and thus only come into action a stage earlier. In larvæ which, for other reasons, must be regarded as more nearly approaching the primitive form, the original

² Persephone, a rare Crab, belonging to the family Leucosidæ, is served in the same manner by its long chelate feet. If we seize the animal, it extends them most obstinately straight downwards, so that in all probability we should more easily break than bend them.

mode usually prevails in this particular also. Thus the caudal feet (the "lateral caudal lamellæ") are formed freely on the ventral surface in *Euphausia* and the Prawns with Nauplius-brood, and within the caudal lamellæ in the Prawns with Zoëa-brood, in *Pagurus* and *Porcellana*.

A compression of several stages into one, and thereby an abridgement and simplification of the course of development, is expressed in the simultaneous appearance of several new pairs of limbs.

How earlier young states may gradually be completely lost, is shown by *Mysis* and the Isopoda. In *Mysis* there is still a trace of the Nauplius-stage; being transferred back to a period when it had not to provide for itself, the Nauplius has become degraded into a mere skin; in *Ligia* (figs. 36, 37) this larva-skin has lost the last traces of limbs, and in *Philoscia* (fig. 38) it is scarcely demonstrable.

Like the spinous processes of the Zoëæ, the chelæ on the penultimate pair of feet of the young Brachyscelus are to be regarded as acquired by the larva itself. The adult animals swim admirably and are not confined to their host; as soon as the specimens of Chrysaora Blossevillei, Less., or Rhizostoma cruciatum, Less., on which they are seated, become the sport of the waves in the neighbourhood of the shore, they escape from them, and are only to be obtained from lively Acalephs. The young are helpless creatures and bad swimmers; a special apparatus for adhesion must be of great service to them.

To review the developmental history of the different Malacostraca in detail would furnish no results at all correspondent to the time occupied by it,—if our knowledge was more complete it would be more profitable. I therefore abandon it, but will not omit to mention that in it many difficulties which cannot at present be satisfactorily solved would present themselves. To these isolated difficulties I ascribe the less importance, however, because even a little while ago, before the discovery of the Prawn-Nauplius, this entire domain of the development of the Malacostraca was almost inaccessible to Darwin's theory.

Nor will I dwell upon the contradictions which appear to result from the application of the Darwinian theory to this department. I leave it to our opponents to find them out. Most of them may easily be proved to be only apparent. There are two of these objections, however, which lie so much on the surface that they can hardly escape being brought forward, and these, I think, I must get rid of.

"The peculiarities in which the Zoëæ of the Crabs, the Porcellanæ, the Tatuira, the Hermit Crabs, and the Prawns with Zoëa-brood agree, and by which they are in common distinguished from the larvæ of Penēus produced from Nauplii, forces us (it might be said) to the supposition that the common ancestor of these various Decapods quitted the egg in a similar Zoëa-form. But then neither Penēus with its Nauplius-brood, nor even apparently the Palinuri could be referred back to this ancestor. The mode of development

of Penëus and Palinurus, as also several peculiar larvæ of unknown origin, but which are in all probability to be attributed to Macrurous Crustacea, necessitate on the contrary the opposite supposition, namely, that the different groups of the Macrura have passed from their original to their present mode of development independently of each other and also independently of the To this we may answer that the occurrence of Crabs." the Zoëa-form in all the above-mentioned Decapoda, its existence in Penëus during the whole of that period of life which is richest in progress and in which the wide gap between the Nauplius and the Decapod is filled up, its recurrence even in the development of the Stomapoda, the occurrence of a larval form closely approaching the youngest Zoëa of Penëus in the Schizopod genus Euphausia, and the reminiscence of the structure of Zoëa, which even the adult Tanais has preserved in its mode of respiration,-all indicate Zoëa as one of those steps in development which persisted as a permanent form throughout a long period of repose, perhaps through a whole series of geological formations, and thus has also made a deeper impression upon the development of its descendants, and formed a firmer nucleus in the midst of other and more readily effaced young states. It cannot, therefore, surprise us that in transitions from the original mode of metamorphosis to direct development, even when produced independently, the larval life commences in the same way with this Zoëa-form in different families, in which the earlier stages of development are effaced. But except what is common to

all Zoëæ, and what may easily be explained as being transferred back from a later into this stage, the Zoëæ of the Crabs, for example, agree with those of Pagurus and Palæmon in no single peculiarity of structure which leads us to suppose a common inheritance. Consequently we may apparently assume, without hesitation, that when the Brachyura and Macrura separated, the primitive ancestors of each of these groups passed through a more complete metamorphosis, and that the transition to the present mode of development belongs to a later period. With regard to the Brachyura, it may be added that in them this transition occurred only a little later and indeed before the existing families separated. The arrangement of the processes of the carapace, and, still more, the similar number of the caudal setæ in the most different Zoëæ of Crabs (figs. 19-23) prove this. Such an accordance in the number of organs apparently so unimportant is only explicable by common inheritance. We may predict with certainty that amongst the Brachyura no species will occur which, like Penëus, still produces Naupliusbrood.8

As we have already seen, Mysis and the Isopoda depart from all other Crustacea very remarkably by the fact that their embryos are curved upwards, instead

³ I must not omit remarking that what has been said as to the development of the Crabs applies essentially only to the groups Cyclometopa, Catometopa and Oxyrhyncha, placed together by Alph. Milne-Edwards as "Eustomés." Among the Oxystomata, as also among the "Anomura apterura," Edw., which approach so nearly to the Crabs, I am unacquainted with the earliest young states of any of the species.

of, as elsewhere, downwards. Does not so isolated a phenomenon as this, it might be asked, in the sense of Darwin's theory, indicate a common inheritance? Does it not necessitate that we should unite as the descendants of the same primitive ancestors, Mysis with the Isopoda on the one hand, and on the other the rest of the Podophthalma with the Amphipoda? I think not. Such a necessity exists only for those who estimate a peculiarity at a higher value because it makes its appearance at an earlier period of the egg-life. regards species as not created independently and unchangeably, but as having gradually become what they are, will say to himself that, when the ancestors of our Mysides came (probably much later than those of the Amphipoda and Isopoda) to develope numerous bodysegments and limbs whilst still embryos, as they could no longer find room in the egg when extended straight out, and were therefore compelled to bend themselves, this could only take place either upwards or downwards, and whatever conditions may have decided the direction actually adopted, any near relationship to either of the two orders of Edriophthalma could hardly have taken part in it.

It may, however, be remarked, that the different curvature of the embryo in the Amphipoda and Isopoda is so far instructive, as it proves that their present mode of development was adopted only after the separation of these orders, and that, in the primitive stock of the Edriophthalma, the embryos were, if not Nauplii, at least short enough in the body to find room in the egg in an

extended position, like the larvæ of Achtheres enclosed by the Nauplius-skin. On the other hand the uniformity of development that prevails in each of the two orders-which is expressed in the Amphipoda for example in the formation of the "micropylar apparatus," in the Isopoda in the want of the last pair of ambulatory feet—testifies that the present mode of development has come down from a very early period and extends back beyond the separation of the present families. In these two orders also, as well as in the Crabs, we can hardly hope to find traces of earlier young states, unless it be in the family of the Tanaidæ.4 If any one will furnish me with an Amphipod or an Isopod with Nauplius-brood, the existence of which would not be more remarkable in independently produced species than that of a Prawn with Nauplius-brood, I will abandon the whole Darwinian theory.

With regard to the Crabs, and also to the Isopoda and Amphipoda, we were led to the assumption, that, about the period when these groups started from the

⁴ Whether the want of the abdominal feet in the young of Tanais be an inheritance from the time of the primitive Isopoda, or a subsequently acquired peculiarity, which appears to me the more admissible view at present, may perhaps be decided with some certainty, when we become acquainted with the development and mode of life of its family allies, Apseudes and Rhau. The latter, as is well known, is the only Isopod which possesses a secondary flagellum on the anterior antennae. I have recently obtained a new and unexpected proof that the Tanaidae ("Asellotes hétéropodes" M.-Edw.) of all known Crustacea approach most closely to the primitive form of the Edriophthalma. Mr. C. Spence Bate writes to me: "Apseudes, as far as I know, is the only Isopod in which the antennal scale so common in the Macrura is present on the lower antennae."

common stem, a simplification of their process of development took place. This also seems to be intelligible from Darwin's theory. When any circumstances favourable to a group of animals caused its wider diffusion and divergence into forms adapting themselves to new and various conditions of existence, this greater variability, which betrays itself in the production of new forms, will also favour the simplification of the development which is almost always advantageous, and moreover, exactly at this period, during adaptation to new circumstances, as has already been indicated with regard to fresh-water animals, this simplification will be doubly beneficial, and therefore, in connexion with this, a doubly strict selection will take place.

So much for the development of the higher Crustacea.

A closer examination of the developmental history of the lower Crustacea is unnecessary after what has been said in general upon the historical significance of the young states, and the application of this which has just been made to the Malacostraca. We may see, without further discussion, how the representation given by Claus of the development of the Copepoda may pass almost word for word as the primitive history of those animals; we may find in the Nauplius-skin of the larvæ of Achtheres and in the egg-like larva of Cryptophialus, precisely similar traces of a transition towards direct development, as were presented by the Nauplius-envelope of the embryos of Mysis and the maggot-like larva of Ligia, &c.

It will be sufficient to indicate an essential difference

in the process of development in the higher and lower Crustacea. In the latter all new body-segments and limbs which insert themselves between the two terminal regions of the Nauplius, are formed in uninterrupted sequence from before backwards; in the former there is further a new formation in the middle of the body (the middle-body), which pushes itself in between the forebody and the abdomen in the same way, as these have done on their part between the head and tail of the Thus, that which appears probable even Nauplius. from the comparison of the limbs of the adult animal, finds fresh support in the developmental history, namely, that the lower Crustacea, like the Insects, are entirely destitute of the region of the body corresponding to the middle-body of the Malacostraca. It seems probable that the swimming feet of the Copepoda, as also of the pupe of Cirripedia and Rhizocephala, represent the abdominal feet of the Malacostraca, that is to say, are derived by inheritance from the same source with them.

It would be easy to weave together the separate threads furnished by the young forms of the various Crustacea, into a general picture of the primitive history of this class. Such a picture, drawn with a little skill, and finished in lively colours, would certainly be more attractive than the dry discussions which I have tacked on to the developmental history of these animals. But the mode of weaving in the loose threads would still in many cases be arbitrary, and to be effected with equal justice in various ways; and many

gaps would still have to be filled up by means of more or less bold assumptions. Those who have not wandered much in this region of research would then readily believe that they were standing upon firm ground, where mere fancy had thrown an airy bridge; those acquainted with the subject, on the other hand, would soon find out these weak points in the structure, but would then be easily led to regard even what was founded upon well considered facts, as merely floating in the air. To obviate these misconceptions of its true contents from either side, it would be necessary to accompany such a picture throughout with lengthy, dry explanations. This has deterred me from further filling in the outline which I had already sketched.

I will only give, as an example, the probable history of the production of a single group of Crustacea, and indeed of the most abnormal of all, the RHIZOCEPHALA, which in the sexually mature state differ so enormously even from their nearest allies, the Cirripedia, and from their peculiar mode of nourishment stand quite alone in the entire animal kingdom.

I must preface this with a few words upon the homology of the roots of the Rhizocephala, i.e. the tubules which penetrate from its point of adhesion into the body of the host, ramify amongst the viscera of the latter, and terminate in cæcal branchlets. In the pupæ of the Rhizocephala (fig. 58) the foremost limbs ("prehensile antennæ") bear, on each of the two terminal joints, a tongue-like, thin-skinned appendage, in which we may generally observe a few small strongly refractive gra-

nules, like those seen in the roots of the adult animal. I have therefore supposed these appendages to be the rudiments of the future roots. A perfectly similar appendage, "a most delicate tube or ribbon," was found by Darwin in free-swimming pupse of Lepas australis on the last joints of the "prehensile antennee." From the perfect accordance in their entire structure shown by the pupse of the Rhizocephala and Cirripedia, there can be no doubt that the appendages of Sacculina and Lepas, which are so like each other and spring from the same spot, are homologous structures.

Now in three species of Lepas, in Dichelaspis Warwickii and in Scalpellum Peronii, Darwin saw, on tearing recently-affixed animals from their point or support, that a long narrow band issued from the same point of the antennæ; its end was torn away, and in Dichelaspis, judging from its ragged appearance, it had attached itself firmly to the support. From this it follows that this appendage in Lepas australis can hardly be anything but a young cement-duct. If, therefore, the supposition that the appendages on the antennæ of the pupe of Rhizocephala are young roots be correct, the roots of the Rhizocephala are homologous with the cement-ducts of the Cirripedia: And this, strange as it may appear at the first glance, seems to me scarcely doubtful. It is true that the act of adhesion of the Rhizocephala has never yet been observed, but it is more than probable that they attach themselves, just like the Cirripedia, by means of the antennæ, and that therefore the points of attachment in the two groups

indicate homologous parts of the body. From the point of attachment in the Rhizocephala the roots penetrate into the body of the host, whilst in the Cirripedia, the cement-ducts issue from the same point. The roots are blind tubes, ramified in different ways in different species. The cement-ducts in the basis of the Balanidæ likewise constitute a generally remarkably complicated system of ramified tubes, with regard to the mode of termination of which nothing certain has yet been made out. Individual cæcal branches are not unfrequently seen even in the vicinity of the carina; and, at least in some species, in which the cement-ducts divide into extremely numerous and fine branchlets, forming a network which gradually becomes denser towards the circumference of the basis, these seem nowhere to possess an orifice.

Now as to the question: How were Cirripedia converted by natural selection into Rhizocephala?

A considerable number of existing Cirripedia settle exclusively or chiefly upon living animals;—on Sponges, Corals, Mollusks, Cetaceans, Turtles, Sea-Snakes, Sharks, Crustaceans, Sea Urchins, and even on Acalephs. *Dichelaspis Darwinii* was found by Filippi in the branchial cavity of *Palinurus vulgaris*, and I have met with another species of the same genus in the branchial cavity of *Lupea diacantha*.

The same thing may have taken place in primitive times. The supposition that certain Cirripedes might once upon a time have selected the soft ventral surface of a Crab, *Porcellana* or *Pagurus*, for its dwelling-place, has certainly nothing improbable about it. If then the cement-ducts of such a Cirripede instead of merely spreading on the surface, pierced or pushed before them the soft ventral skin and penetrated into the interior of the host, this must have been beneficial to the animal, because it would be thereby more securely attached and protected from being thrown off during the moulting of its host. Variations in this direction were preserved as advantageous.

But as soon as the cement-ducts penetrated into the body-cavity of the host and were bathed by its fluids, an endosmotic interchange must necessarily have been set up between the materials dissolved in these fluids and in the contents of the cement-ducts, and this interchange could not be without influence upon the nourishment of the parasite. The new source of nourishment opened up in this manner was, as constantly flowing, more certain than that offered by the nourishment accidentally whirled into the mouth of the sedentary animal. The individuals favoured in the development of the cement-ducts now converted into nutriferous roots, had more than others the prospect of abundant food, of vigorous growth, and of producing a numerous progeny. With the further development, assisted by natural selection, of the roots embracing the intestine of the host and spreading amongst its hepatic tubes, the introduction of nourishment through the mouth and all the parts implicated in it, such as the whirling cirri, the buccal organs, and the intestine, gradually lost their importance, became aborted by disuse, and finally disappeared without leaving a trace of their existence. Protected by the abdomen of the Crab, or by the shell inhabited by the *Pagurus*, the parasite also no longer required the calcareous test, in which, no doubt, the first Cirripedes settling upon these Decapods rejoiced. This protective covering, having become superfluous, also disappeared, and there remained at last only a soft sack filled with eggs, without limbs, without mouth or alimentary canal, and nourished, like a plant, by means of roots, which it pushed into the body of its host. The Cirripede had become a Rhizocephalon.

If it be desired to form a notion of what our parasite may have looked like when half way in its progress from the one form to the other, we may consult the figures given by Darwin, (Lepadidæ Pl., iv., figs. 1-7) of Anelasma squalicola. This Lepadide, which lives upon Sharks in the North Sea, seems, in fact, to be in the best way to lose its cirri and buccal organs in the same manner. The widely-cleft, shell-less test is supported upon a thick peduncle, which is immersed in the skin of the Shark. The surface of the peduncle is beset with much-ramified, hollow filaments, which "penetrate the Shark's flesh like roots" (Darwin). Darwin looked in vain for cement-glands and cement. It seems to me hardly doubtful, that the ramified hollow filaments are themselves nothing but the cement-ducts converted into nutritive roots, and that it is just in consequence of the development of this new source of nourishment, that the cirri and buccal organs are in the highest degree aborted. All the parts of the mouth are extremely

minute; the palpi and exterior maxillæ have almost disappeared; the cirri are thick, inarticulate, and destitute of bristles; and the muscles both of the mouth and cirri are without transverse striation. Darwin found the stomach perfectly empty in the animal examined by him.

Having reached the Nauplius, the extreme outpost of the class, retiring furthest into the gray mist of primitive time, we naturally look round us to see whether ways may not be descried thence towards other bordering regions. By the structure of the abdomen in Nauplius we might be reminded, like Oscar Schmidt, of the moveable caudal fork of the Rotatoria, which many regard as near allies of the Crustacea, or at any rate of the Arthropoda; in the six feet surrounding the mouth we might imagine an originally radiate structure, and so forth. But I can see nothing certain. Even towards the nearer provinces of the Myriopoda and Arachnida I can find no bridge. For the Insecta alone, the development of the Malacostraca may perhaps present a point of union. Like many Zoëæ, the Insecta possess three pairs of limbs serving for the reception of nourishment, and three pairs serving for locomotion; like the Zoëæ they have an abdomen without appendages; as in all Zoëæ the mandibles in Insects are destitute of palpi. Certainly but little in common, compared with the much which distinguishes these two animal-forms. Nevertheless the supposition that the Insecta had for their common ancestor a Zoëa which raised itself into a life on land, may be recommended for further examination.

Much in what has been adduced above may be erroneous, many an interpretation may have failed, and many a fact may not have been placed in its proper light. But in one thing, I hope, I have succeeded,—in convincing unprejudiced readers, that Darwin's theory furnishes the key of intelligibility for the developmental history of the Crustacea, as for so many other facts inexplicable without it. The deficiencies of this attempt, therefore, must not be laid to the charge of the plan drawn out by the sure hand of the master, but solely to the clumsiness of the workman, who did not know how to find the proper place for every portion of his material.