CHAPTER VIII.

DEVELOPMENTAL HISTORY OF EDRIOPHTHALMA.

LESS varied than that of the Stalk-eyed Crustacea is the mode of development of the Isopoda and Amphipoda, which Leach united in the section Edriophthalma, or Crustacea with sessile eyes.

The Rock-Slaters (*Ligia*) may serve as an example of the development of the Isopoda. In these, as in *Mysis*, the caudal portion of the embryo is bent not downwards, but upwards; as in *Mysis* also, a larval membrane is first of all formed, within which the Slater is developed. In *Mysis* this first larval skin may be compared to a Nauplius; in *Ligia* it appears like a maggot quite destitute of appendages, but produced into a long simple tail (fig. 37). The egg-membrane is retained longer than in *Mysis;* it bursts only when the limbs of the young Slater are already partially developed in their full number. The dorsal sur-

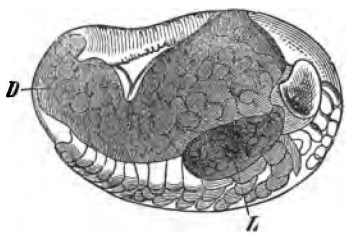


Fig. 36.[1]

[1] Fig. 36. Embryo of *Ligia* in the egg, magn. 15 diam. *D.* yelk; *L.* liver.

face of the Slater is united to the larval skin a little behind the head. At this point, when the union has been dissolved a little before the change of skin, there is a foliaceous appendage, which exists only for a short time, and disappears before the young Slater quits the brood-pouch of the mother.

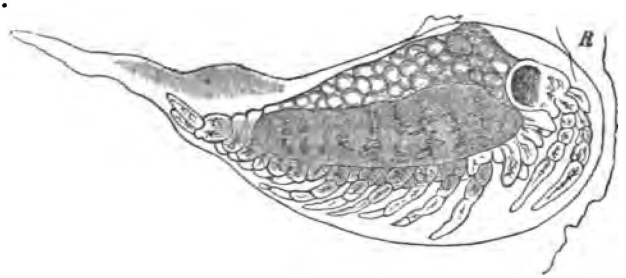


Fig. 37.[2]

The young animal, when it begins to take care of itself, resembles the old ones in almost all parts, except one important difference; it possesses only six, instead of seven pairs of ambulatory feet; and the last segment of the middle-body is but slightly developed and destitute of appendages. It need hardly be mentioned that the sexual peculiarities are not yet developed, and that in the males the handlike enlargements of the anterior ambulatory feet and the copulatory appendages are still deficient.

[2] Fig. 37. Maggot-like larva of *Ligia*, magn. 15 diam. *R.* remains of the egg-membrane. We see on the lower surface, from before backwards:—the anterior and posterior antennæ, the mandibles, the anterior and posterior maxillæ, maxillipedes, six ambulatory feet, the last segment of the middle-body destitute of appendages, five abdominal feet, and the caudal feet.

To the question, how far the development of *Ligia* is repeated in the other Isopoda, I can only give an unsatisfactory answer. The curvature of the embryo upwards instead of downwards was met with by me as well as by Rathke in *Idothea*, and likewise in *Cassidina*, *Philoscia*, *Tanais*, and the Bopyridæ,—indeed, I failed to find it in none of the Isopoda examined for this purpose. In *Cassidina* also the first larval skin without appendages is easily detected; it is destitute of the long tail, but is strongly bent in the egg, as in *Ligia*, and consequently cannot be mistaken for an "inner egg-membrane." This, however, might happen in *Philoscia*, in which the larval skin is closely applied to the egg-membrane (fig. 38), and is only to be explained as the larval skin by a reference to *Ligia* and *Cassidina*.

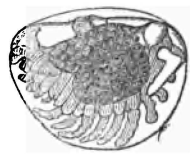


Fig. 38.[3]

The foliaceous appendage on the back has long been known in the young of the common Water Slater (*Asellus*).[4] That the last pair of feet of the thorax

[3] Fig. 38. Embryo of a *Philoscia* in the egg, magn. 25 diam.

[4] Leydig has compared this foliaceous appendage of the Water Slaters with the "green gland" or "shell-gland" of other crustacea, assuming that the green gland has no efferent duct and appealing to the fact that the two organs occur "in the same place." This interpretation is by no means a happy one. In the first place we may easily ascertain in *Leucifer*, as was also found to be the case by Claus, that the "green gland" really opens at the end of the process described by Milne-Edwards as a "tubercule auditif" and by Spence Bate as an "olfactory denticle." And, secondly, the position is about as different as it can well be. In the one case a paired gland, opening at the base of the posterior antennæ, and therefore on the lower surface of the *second* segment; in the other an unpaired structure rising

is wanting in the young of the Wood-lice (*Porcellionides*, M.-Edw.) and Fish-lice (*Cymothoadiens*, M.-Edw.) has already been noticed by Milne-Edwards. This applies also to the Box-Slaters (*Idothea*), to the viviparous Globe-Slaters (*Sphæroma*) and Shield-Slaters (*Cassidina*), to the Bopyridæ (*Bopyrus, Entoniscus, Cryptoniscus*, n. g.), and to the Cheliferous Slaters (*Tanais*), and therefore probably to the great majority of the Isopoda. All the other limbs are usually well developed in the young Isopoda. In *Tanais* alone, all the abdominal feet are wanting (but not those of the tail); they are developed simultaneously with the last pair of feet of the thorax.

The last pair of feet on the middle-body of the larva, consequently the penultimate pair in the adult animal, is almost always similar in structure to the preceding pair. A remarkable exception is, however, presented in this respect by *Cryptoniscus* and *Entoniscus*,— remarkable as a confirmation of Darwin's proposition that "parts developed in an unusual manner are very variable," for in the peculiarly-formed pair of feet there exists the greatest possible difference between the three species hitherto observed. In *Cryptoniscus* (fig. 39) this last foot is thin and rod-like; in *Entoniscus Can-*

Fig. 39.[5]

Fig. 40.[6]

in the median line of the back *behind the seventh segment*, ("behind the boundary line of the first thoracic segment," Leydig).

[5] Fig. 39. Embryo of *Cryptoniscus planarioïdes*, magn. 90 diam.

[6] Fig. 40. Last foot of the middle-body of the larva of *Entoniscus Porcellanæ*, magn. 180 diam.

ororum remarkably long and furnished with a strongly thickened hand and a peculiarly constructed chela; in *Entoniscus Porcellanæ* very short, imperfectly jointed, and with a large ovate terminal joint (fig. 40).

Some Isopods undergo a considerable change immediately before the attainment of sexual maturity. This is the case with the males of *Tanais* which have already been noticed, and, according to Hesse, with the *Praniza*, in which both sexes are said to pass into the form known as *Anceus*. But Spence Bate, a careful observer, states that he has seen females of the form of *Praniza* laden with eggs far advanced in their development.

In this order we meet for the first time with an extensive retrograde metamorphosis as a consequence of a parasitic mode of life. Even in some Fish-lice (*Cymothoa*) the young are lively swimmers, and the adults stiff, stupid, heavy fellows, whose short clinging feet are capable of but little movement. In the Bopyridæ (*Bopyrus, Phryxus, Kepone*, &c., which might have been conveniently left in a single genus), which are parasitic on Crabs, Lobsters, &c., taking up their abode chiefly in the branchial cavity, the adult females are usually quite destitute of eyes; the antennæ are rudimentary; the broad body is frequently unsymmetrically developed in consequence of the confined space; its segments are more or less amalgamated with each other; the feet are stunted, and the appendages of the abdomen transformed from natatory feet with long setæ into foliaceous or tongue-shaped and sometimes ramified branchiæ. In the dwarfish males the

eyes, antennæ, and feet, are usually better preserved than in the females; but on the other hand all the appendages of the abdomen have not unfrequently disappeared, and sometimes every trace of segmentation. In the females of *Entoniscus*, which are found in the body-cavity of Crabs and *Porcellanæ*, the eyes, antennæ, and buccal organs, the segmentation of the vermiform body, and in one species (fig. 41) the whole of the limbs, disappear almost without leaving a trace; and *Cryptoniscus planarioïdes* would almost be regarded as a Flatworm rather than an Isopod, if its eggs and young did not betray its Crustacean nature. Among the males of these various Bopyridæ, that of *Entoniscus Porcellanæ* occupies the lowest place; it is confined all its life to six pairs of feet, which are reduced to shapeless rounded lumps.

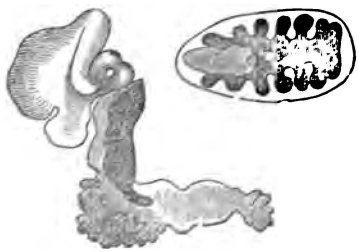


Fig. 41.[7] Fig. 42.[8]

Fig. 43.[9]

The Amphipoda are distinguishable from the Isopoda at an early period in the egg by the different position of the embryo, the hinder extremity of which is bent downwards. In all the ani-

[7] Fig. 41. *Entoniscus Cancrorum*, female, magn. 3 times.
[8] Fig. 42. *Cryptoniscus planarioïdes*, female, magn. 3 times.
[9] Fig. 43. Embryo of a *Corophium*, magn. 90 diam.

mals of this order which have been examined for it,[10] a peculiar structure makes its appearance very early on the anterior part of the back, by which the embryo is attached to the "inner egg-membrane," and which has been called the "micropylar apparatus," but improperly as it seems to me.[11] It will remind us of the union of the young Isopoda with the larval membrane and of the unpaired "adherent organ" on the nape of the Cladocera, which is remarkably developed in *Evadne* and persists throughout life; but in *Daphnia pulex*, according to Leydig, although present in the young animals, disappears without leaving a trace in the adults.

The young animal, whilst still in the egg, acquires the full number of its segments and limbs. In cases where segments are amalgamated together, such as the last two segments of the thorax in *Dulichia*, the last abdominal segments and the tail in *Gammarus ambulans* and *Coro-*

[10] In the genera *Orchestoidea*, *Orchestia*, *Allorchestes*, *Montagua*, *Batea* n. g., *Amphilochus*, *Atylus*, *Microdeutopus*, *Leucothoë*, *Melita*, *Gammarus* (according to Meissner and La Valette), *Amphithoë*, *Cerapus*, *Cyrtophium*, *Corophium*, *Dulichia*, *Protella* and *Caprella*.

[11] Little as a name may actually affect the facts, we ought certainly to confine the name "micropyle" to canals of the egg-membrane, which serve for the entrance of the semen. But the outer egg-membrane passes over the "micropylar apparatus" of the Amphipoda without any perforation, according to Meissner's and La Valette's own statements; it appears never to be present before fecundation, attains its greatest development at a subsequent period of the ovular life, and the delicate canals which penetrate it do not even seem to be always present, indeed it seems to belong to the embryo rather than to the egg-membrane. I have never been able to convince myself that the so-called "inner egg-membrane" is really of this nature, and not perhaps the earliest larva skin, not formed until after impregnation, as might be supposed with reference to *Ligia*, *Cassidina* and *Philoscia*.

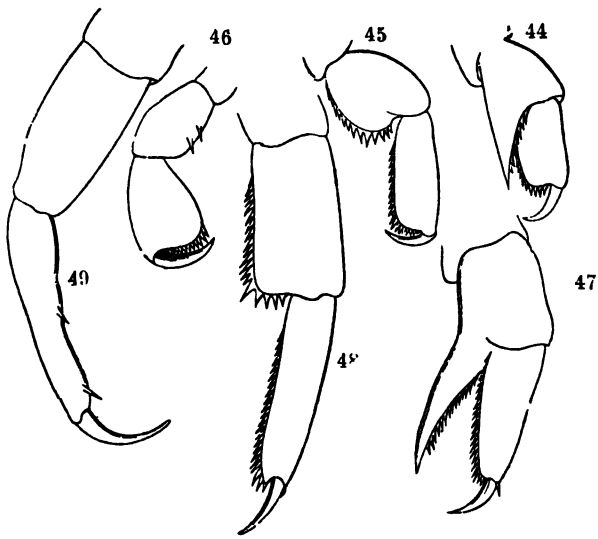
phium dentatum, n. sp., and the last abdominal segments and the tail in *Brachyscelus*,[12] or where one or more segments are deficient, as in *Dulichia* and the *Caprellæ*, we find the same fusion and the same deficiencies in young animals taken out of the brood-pouch of their mother. Even peculiarities in the structure of the limbs, so far as they are common to both sexes, are usually well-marked in the newly hatched young, so that the latter generally differ from their parents only by their stouter form, the smaller number of the antennal joints and olfactory filaments, and also of the setæ and teeth with which the body or feet are armed, and perhaps by the comparatively larger size of the secondary flagellum. An exception to this rule is presented by the Hyperinæ which usually live upon Acalephæ. In these the young and adults often have a remarkably different appearance; but even in these there is no new formation of body-segments and limbs, but only a gradual transformation of these parts.[13]

[12] According to Spence Bate, in *Brachyscelus crusculum* the fifth abdominal segment is not amalgamated with the sixth (the tail) but with the fourth, which I should be inclined to doubt, considering the close agreement which this species otherwise shows with the two species that I have investigated.

[13] In the young of *Hyperia galba* Spence Bate did not find any of the abdominal feet, or the last two pairs of thoracic feet, but this very remarkable statement required confirmation the more because he examined these minute animals only in the dried state. Subsequently I had the wished-for opportunity of tracing the development of a *Hyperia* which is not uncommon upon Ctenophora, especially *Beroë gilva*, Eschsch. The youngest larvæ from the brood-pouch of the mother already possess *the whole* of the thoracic feet; on the other hand, like Spence Bate, I cannot find those of the abdomen. At first simple enough, all these feet soon become converted, like the anterior

Thus, in order to give a few examples, the powerful chelæ of the antepenultimate pair of feet, of *Phromina*

feet, into richly denticulated prehensile feet, and indeed of three different forms, the anterior feet (fig. 44) the two following pairs (fig. 45) and finally the three last pairs (fig. 46) being similarly constructed and different from the rest. In this form the feet remain for a very long time, whilst the abdominal appendages grow into powerful natatory organs, and the eyes, which at first seemed to me to be wanting, into large hemispheres. In the transition to the form of the adult animal the last three pairs of feet (fig. 49) especially undergo a con-



Figs. 44—49.[a]

[a] Figs. 44–46. Feet of a half-grown *Hyperia Martinezii*, n. sp.[b] Figs. 47–49. Feet of a nearly adult male of the same species; 44 and 47 from the first pair of anterior feet (gnathopoda); 44 and 48 from the first, and 46 and 49 from the last pair of thoracic feet. Magn. 90 diam.

[b] Named after my valued friend the amiable Spanish zoologist, M. Francisco de Paula Martinez y Saes, at present on a voyage round the world.

sedentaria, are produced, according to Pagenstecher, from simple feet of ordinary structure; and *vice versâ*, the chelæ on the penultimate pair of feet of the young *Brachyscelus*, become converted into simple feet. In the young of the last-mentioned genus the long head is drawn out into a conical point and bears remarkably small eyes; in course of growth, the latter, as in most of the Hyperinæ, attain an enormous size, and almost entirely occupy the head, which then appears spherical, &c.

The difference of the sexes which, in the Gammarinæ is usually expressed chiefly in the structure of the

siderable change. The difference between the two sexes is considerable; the females are distinguished by a very broad thorax, and the males (*Lestrigonus*) by very long antennæ, of which the anterior bear an unusual abundance of olfactory filaments.

Their youngest larvæ of course cannot swim; they are helpless little animals which firmly cling especially to the swimming laminæ of their host; the adult *Hyperiæ*, which are not unfrequently met with free in the sea, are, as is well known, the most admirable swimmers in their order. ("Il nage avec une rapidité extrême," says Van Beneden of *H. Latreillii* M.-Edw.)

The transformation of the *Hyperiæ* is evidently to be regarded as *acquired* and not *inherited*, that is to say the late appearance of the abdominal appendages and the peculiar structure of the feet in the young are not to be brought into unison with the historical development of the Amphipoda, but to be placed to the account of the parasitic mode of life of the young.

As in *Brachyscelus*, free locomotion has been continued to the adult and not to the young, contrary to the usual method among parasites. Still more remarkable is a similar circumstance in *Caligus*, among the parasitic Copepoda. The young animal, described by Burmeister as a peculiar genus, *Chalimus*, lies at anchor upon a fish by means of a cable springing from its forehead, and having its extremity firmly seated in the skin of the fish. When sexual maturity is attained, the cable is cut, and the adult *Caligi*, which are admirable swimmers, are not unfrequently captured swimming freely in the sea. (See 'Archiv. für Naturg.' 1852, I. p. 91).

anterior feet (gnathopoda, Sp. Bate) and in the Hyperinæ in the structure of the antennæ, is often so great that males and females have been described as distinct species, and even repeatedly placed in different genera (*Orchestia* and *Talitrus*, *Cerapus* and *Dercothoë*, *Lestrigonus* and *Hyperia*) or even families (*Hypérines anormales* and *Hypérines ordinaires*). Nevertheless it is only developed when the animals are nearly full-grown. Up to this period the young resemble the females in a general way, even in some cases in which these differ more widely than the males from the "Type" of the order. Thus in the male Shore-hoppers (*Orchestia*) the second pair of the anterior feet is provided with a powerful hand, as in the majority of the Amphipoda, but very differently constructed in the females. The young, nevertheless, resemble the female. Thus also,—and this is an extremely rare case,[14]—the females of *Brachyscelus* are destitute of the posterior (or inferior) antennæ; the male possesses them like other Amphipodæ; in the young I, like Spence Bate, can find no trace of them.

It is, however, to be particularly remarked, that the development of the sexual peculiarities does not stand still on the attainment of sexual maturity.

For example, the younger sexually mature males of *Orchestia Tucurauna*, n. sp., have slender inferior antennæ, with the joints of the flagellum not fused together, the clasping margin ("palm," Sp. Bate) of the

[14] "I know of no case in which the inferior (antennæ) are obsolete, when the superior are developed," Dana. (Darwin, 'Monograph on the Subclass Cirripedia, Lepadidæ,' p. 15.)

hand in the second pair of feet is uniformly convex, the last pair of feet is slender and similar to the preceding. Subsequently the anteunæ become thickened, two, three, or four of the first joints of the flagellum are fused together, the palm of the hand acquires a deep emargination near its inferior angle, and the intermediate joints of the last pair of feet become swelled into a considerable incrassation. No museum-zoologist would hesitate about fabricating two distinct species, if the oldest and youngest sexually mature males were sent to him without the uniting intermediate forms. In the younger males of *Orchestia Tucuratinga*, although the microscopic examination of

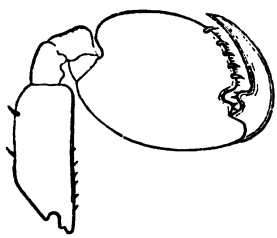


Fig. 50.[15]

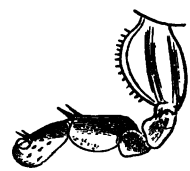


Fig. 51.[15]

their testes showed that they were already sexually mature, the emargination of the clasping margin of the hand (represented in fig. 50) and the corresponding process of the finger, are still entirely wanting. The same may be observed in *Cerapus* and *Caprella*, and probably in all cases where hereditary sexual differences occur.

[15] Fig. 50. Foot of the second pair ("second pair of gnathopoda") of the male and fig. 51 of the female, of *Orchestia Tucuratinga*, magn. 15 diam.

Next to the extensive sections of the Stalk-eyed and Sessile-eyed Crustacea, but more nearly allied to the former than to the latter, comes the remarkable family of the *Diastylidæ* or *Cumacea*. The young, which Kröyer took out of the brood-pouch of the female, and which attained one-fourth of the length of their mother, resembled the adult animals almost in all parts. Whether, as in *Mysis* and *Ligia*, a transformation occurs within the brood-pouch, which is constructed in the same way as in *Mysis*, is not known.[17] The caudal

Fig. 52.[16]

[16] Fig. 52. Male of a *Bodotria*, magn. 10 diam. Note the long inferior antennæ, which are closely applied to the body, and of which the apex is visible beneath the caudal appendages.

[17] A trustworthy English Naturalist, Goodsir, described the brood-pouch and eggs of *Cuma* as early as 1843. Kröyer, whose painstaking care and conscientiousness is recognised with wonder by every one who has met him on a common field of work, confirmed Goodsir's statements in 1846, and, as above mentioned, took out of the brood-pouch embryos advanced in development and resembling their parents. By this the question whether the Diastylidæ are full-grown animals or larvæ, is completely and for ever set at rest, and only the famous names of Agassiz, Dana and Milne-Edwards, who would recently reduce them again to larvæ (see Van Beneden, 'Rech. sur la Faune littor. de Belgique,' Crustacées, pp. 73, 74), induce me, on the basis of numerous investigations of my own, to declare in Van Beneden's words; "Parmi toutes les formes embryonnaires de podophthalmes ou d'édriophthalmes que nous avons observées sur nos côtes, nous n'en avons pas vu une seule qui eût même la moindre ressemblance avec un *Cuma* quelconque." The *only thing* that suits the larvæ of *Hippolyte*, *Palæmon* and *Alpheus*, in the family character of the Cumacea as given by Kröyer which occupies three pages (Kröyer, 'Naturh. Tidsskrift, Ny Række,' Bd. ii. pp. 203—206) is: "Duo antennarum paria." And this, as is well known

portion of the embryo in the *Diastylidæ*, as I have recently observed, is curved upwards as in the Isopoda, and the last pair of feet of the thorax is wanting.

Equally scanty is our knowledge of the developmental history of the Ostracoda. We know scarcely anything except that their anterior limbs are developed before the posterior one (Zenker). The development of *Cypris* has recently been observed by Claus:—"The youngest stages are shell-bearing Nauplius-forms."

applies to nearly all Crustacea. How well warranted are we therefore in identifying the latter with the former. However, it is sufficient for any one to glance at the larva of *Palæmon* (fig. 27) and the Cumacean (fig. 52) in order to be convinced of their extraordinary similarity!