XVII. On the supposed existence of Metamorphoses in the Crustacea. By J. O. West wood, F.L.S. & Sec. Ent. Soc. Communicated by J. G. Children, Esq., Sec. R.S.

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PERHAPS none of the phenomena of natural history have attracted a greater share of the attention of mankind in all ages than those exhibited by insects in their passage to the perfect state, and to which it is not surprising that the name of metamorphoses should have been applied. If this were the case in the darker days of zoological knowledge, when the true nature of these changes was not understood, it is not strange that the subject should have lost none of its interest when, owing to the admirable researches of Redi and Swammerdam, De Geer and Reaumur, all of the marvellous has been removed, and a series of gradual developments exposed, far exceeding in peculiarity those exhibited in any of the other tribes of animals.

It will not perhaps be considered out of place if we here shortly glance at those general principles which regulate these metamorphoses amongst the *Annulosa*. "Si nous voulons concevoir," observes Latreille, "d'une manière claire et positive le sens qu'il faut attacher au mot de *métamorphose*, il est necessaire que nous nous formions une idée exacte de celui de *mue*; car leurs significations paraissent avoir beaucoup d'affinité, et il est essentiel de les déterminer aussi rigoureusement qu'il est possible*."

It would, however, lead us to far too great a length were we at the outset to enter into the question of the gradual formation of the various organs of annulose animals from the rete mucosum, as insisted upon by Dr. Heroldt in opposition to the generally received opinion of Swammerdam, that these various organs are, from the first exclusion of the insect from the egg, in a state of existence, but enveloped in various coverings which are successively cast off; although the determination of this question must be considered as having a material influence upon the subject under consideration, more especially as it seems difficult to account for the reproduction of the limbs of the Crustacea when torn off if we do not adopt the theory of Dr. Heroldt.

Every animated being in its passage to the perfect development of its species undergoes a certain but varied series of changes. In man and most of the vertebrated animals there is a gradual action of the vital forces in different organs till they are fitted for reproduction, accompanied, as progress is made to the adult state, by the acquisition of various appendages, as teeth, horns, pubes, feathers, &c. In addition

* Cours d'Entomologie, p. 271.

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to this gradual action, the greater portion of the Vertebrata are subject to that particular species of ecdysis which Mr. MacLean has termed incomplete, consisting simply in the integuments, hairs, skin, feathers, &c., scaling off piece by piece, or one by one, as distinguished from that complete change in the identity of the envelope of other less perfect animals which prevails in various degrees amongst the Annulosa and some few of the Vertebrata, and by means of which the entire envelope of the animal is shed at once. And here we may be allowed to notice the rationale of this complete shedding of the envelope which so peculiarly distinguishes the Annulosa. In them we find the internal vertebræ of the higher animals converted into a hard horny or crustaceous external covering, to the inner surface of which the muscles are attached. This covering would of course, from its very nature, offer an insurmountable obstacle against the growth of the animal, were it persistent. It is therefore necessary that, in order to ensure the due increase of size in the animal, its old covering should be cast off and a new and enlarged one obtained. And this is what takes place throughout the Annulosa, the shedding of the shell of the Lobster and the moulting of the Caterpillar being but modified examples of the same principle.

These modifications may be reduced to three principal heads, of which the Spider, the Grasshopper, and the Butterfly may be cited as well-known examples.

In the first of these, the animal is produced from the egg in a form which it is destined to retain throughout its existence, its only change consisting in a series of moultings of the outer envelope, by which an increase of size, but not an addition of new organs, is acquired.

In the second, the animal at its exclusion exhibits the form which it retains through life, but it is subject to a series of moultings, during several of the last of which certain new organs are gradually developed.

In the third, the form of the animal at its exclusion from the egg is totally different from that in which it appears in its image state, this change of form taking place during two or three of its final moultings, and consisting not only in the variation of the form of the body, but also in a complete change in the nutritive and digestive systems, and in the acquisition of various new organs. This constitutes what has generally been termed metamorphosis.

Now, since the *Ptilota* of Aristotle are preeminently the types of the invertebrated animals, and as such more distantly removed from the various groups of the *Vertebrata* than the remainder of the *Invertebrata*, (owing this preeminence not only to the superiority of their instincts, but also to the development of organs of flight during the latter moultings,) it will necessarily follow that those *Annulosa* which are less typical, or, in other words, more nearly allied to the lowest of the higher groups of animals, will not exhibit in so remarkable a degree those metamorphoses which, as we have seen, the *Ptilota* so peculiarly undergo.

Hence, since the organization of the Crustacea is more clearly analogous to that of the Vertebrata than that of the Ptilota, we arrive at one of the chief grounds for the

generally received opinion amongst naturalists, that the transformations of the *Crustacea* consist merely in the periodical shedding of the outer envelope, without any metamorphosis being undergone or additional organs acquired.

The object of the following pages is therefore to endeavour to ascertain whether this opinion be correct or not; and in order to do this satisfactorily we shall be obliged to test such observations which may negative its correctness, by the application of those general principles which, as we have seen, regulate the transformations or other changes of the *Annulosa*.

The non-existence of transformations in the *Crustacea* in general has been asserted by every crustaceologist, with the exception of a recent author, John V. Thompson, Esq., F.L.S., (the accuracy of whose beautiful figures deserves the highest praise,) and by whom, in the first and succeeding numbers of the Zoological Researches, the discovery that the greater number of the *Crustacea* do actually undergo metamorphoses of a very peculiar kind, and of a totally different description from those of insects, has been announced. "So little has this been suspected by naturalists," observes this author*, "that the contrary has been assigned as one of the distinctive characters of the class, and been used as an argument for their separation from insects."

Mr. Thompson's views are founded upon some circumstances exhibited by some of the most singular animals hitherto ascertained to belong to the class, (which constitute the genus Zoea of Bosc,) as recorded by Slabber or Mr. Thompson himself, as well as upon some other circumstances respecting other portions of the class. These consist,

In the first place, in a supposed change which the Zoes are reputed to undergo; respecting which Mr. Thompson (after alluding to the observations of Slabber, which he thinks erroneous,) thus expresses himself: "After keeping a full-grown Zoe for more than a month, it died in the act of changing its skin and of passing into a new form, but one by no means similar to that expected [from the previous observations of Slabber], as appears evidently by its disengaged members, which are changed in number as well as in form, and now correspond with those of the Decapoda (Crabs, &c.), viz. five pair, the anterior of them furnished with a large claw or pincer: the metamorphosis not having been completed, prevented any knowledge being acquired of its general form; enough, however, has been gained to show that the distinctive characters of Zoea and of Slabber's changed Zoea were entirely lost; that the members, from being natatory and cleft (as shall shortly be shown), become simple and adapted to crawling only. On the 1st of May another large Zoea was taken, and dying towards the end of the month without having the strength to disengage itself from the exuvium, presented precisely the same results with the former ." In the account of the figures of this full-grown Zoe, "behind the corselet the rudiments of the limbs of the perfect animal, or Crab," are described as "beginning to show themselves;" but on comparing this figure with that of the newly hatched "Zoe,

or larva of the common or edible Crab," (Pl. VIII. fig. 1.) "the disparity in size is shown between a Zoe newly hatched and one which has attained its full development, and the changes which the various parts undergo during the growth of the animal," (No. 2. Addendum,) as in the total absence of subabdominal fins, and in the natatory division of the two pairs of feet having only four plumose setæ in the younger animal: and in a former passage he observes, that "the larger specimens may be supposed to differ from such as occur of smaller size in the greater degree of development of all its parts; thus, the eyes are more distinctly pedunculate, the natatory division of the feet have an increased number of plumose setæ, the rudiments of the subabdominal fins are quite obvious, and the mandibles show the rudiment of a palp: in other respects they are essentially the same." (p. 10.)

In the second place, our author states that he had succeeded in hatching the ova of the common Crab (Cancer Pagurus), which presented exactly the appearance of Zoea Taurus, with the addition of lateral spines to the corselet. And in the addenda to his second number he has again stated this circumstance, adding somewhat more precisely, that he had protected a female Crab with spawn apparently ready to hatch until the young burst from their envelopes and swam about in myriads under the exact form of Zoea represented in the Plate.

In the third place, Mr. Thompson has stated that the common Lobster undergoes metamorphosis, "but less in degree" than any of the other genera in which he states that he had observed this to take place, and "consisting in a change from a cheliferous Schizopode to a Decapode, in its first stage being what I call a modified Zoe, with a frontal spine, a spatulate tail, and wanting subabdominal fins, in short, such an animal as would never be considered what it really is, were it not obtained by hatching the spawn of the Lobster*."

The only figure which accompanies this remark is given in tab. xv. fig. 13. of the same work, of "the cheliferous member of the larva of the Lobster, in which a is the claw; b, the outer division of the limb, or future flagrum; and c, the rudimentary branchia." In this figure, three organs are represented as arising from a large basal joint: first, the chelate organ, composed of two joints and a large didactyle chela; second, a three-jointed organ, of which the terminal joint is long, slender, and strongly setose; and third, a small rudimental branchia.

In the fourth place, "this curious piece of economy," according to Mr. Thompson, "explains what has ever appeared paradoxical to naturalists, viz. the annual peregrinations of the land Crabs to the sea-side, which, although acknowledged to be true by several competent observers, could never before be satisfactorily accounted for." (p. 9.) And again, in the Addenda to his second number: "Hitherto the rationale of this long and dangerous journey did not appear; naturalists have thought it strange that an animal entirely terrestrial should not spawn in its native haunts, and rear its young at home, instead of putting them to the trouble of a tedious and unknown

^{*} Zoological Journal, No. xix. p. 383.

route back again in their very tender age. Scarcely a stronger confirmation than this very circumstance, of the universality of metamorphosis, could be adduced: for if there were any exception, it would be in the terrestrial species; but no, they are, when first hatched, incapable of living out of water with swimming members; hence the parent is impelled by instinct to seek that element for its progeny which Nature has designed for the whole of the tribe to which they belong. Having lived amongst West Indian islands, where these facts were constantly before him, neither he, nor any other person, could invent any plausible reason for this curious piece of economy."

In the fifth and last place are to be noticed Mr. Thompson's general statements. In the Addenda to his second number he states that he has had a confirmation of his views in one of the West Indian land Crabs, and in some other of our most widely separated native genera, authorizing his previous assertion that the greater number of the Crustacea do actually undergo transformations, of which, in addition to the facts adduced in his first memoir, further instances will be given in future memoirs. On the wrapper of his fourth number he has given a list of some of these promised memoirs, in which we find the Paguri, the Shrimp and Prawn, the genera Porcellana, Gegarcinus, Hydrodomus, and other genera of land Crabs and Pinnotheres, all stated to undergo various remarkable metamorphoses; and in the nineteenth number of the Zoological Journal he states that the newly hatched young of the following Brachyurous genera, Cancer, Carcinus, Portunus, Eryphia, Gegarcinus, Thelphusa?, Pinnotheres, and Inachus, have been ascertained to be Zoes by himself; and that the following Macrourous genera are likewise subject to metamorphosis, viz. Pagurus, Porcellana, Galathea, Crangon, Palemon, Homarus, Astacus.!

Such are the various circumstances upon which Mr. Thompson has built his theory of metamorphosis. I have given them at rather an inconvenient, but not an unnecessary length, and as far as possible in his own words, in order that I might be free from any charge of misrepresentation in the observations which I may think it necessary to make upon each of them, with a view to prove that the theory is without foundation.

For this purpose I propose, in the first place, to enter into a review of Mr. Thompson's observations, whence alone I conceive that no sufficient ground is raised for the establishment of the theory in question. In the second place, I propose to collect the recent views of the most celebrated crustaceologists, all of whom have advanced opinions to the like effect. And in the third place, I shall bring forward some circumstances observed by myself having a precisely similar tendency.

In the first place, therefore, I have to endeavour to prove from Mr. Thompson's own statements and figures, that there is not sufficient foundation for the theory of metamorphosis, and for this purpose I shall take in review *seriatim* the several circumstances which he has mentioned and above alluded to.

And first with respect to the metamorphosis into Crabs which the Zoes are stated to undergo, against which six arguments may be adduced.

- 1. It is to be observed that the account given of the mode in which this metamorphosis is supposed to be effected, is as vague and indefinite as it is possible to be. It is stated that the Zoe died in the act of casting its skin, but its metamorphosis not being completed, prevented any knowledge being acquired of its general form; and yet it is added that five pairs of legs had become disengaged, and that the characters of Zoea were entirely lost. Plate II. fig. 2., however, proves nothing like this. The limbs of the future Crab are asserted to be beginning to show themselves, and yet the Zoe retains its original form, without losing a single character which it previously possessed,—without our being able to trace the least appearance of the animal having commenced the shedding of the skin,—or without our being able to gain the least idea how "the members, from being natatory and cleft (as shall shortly be shown), become simple and adapted to crawling only." But Mr. Thompson has omitted to fulfill this promise, which, if it mean anything, must be understood as an assertion that the two pairs of natatory and cleft legs are transformed into five pairs of simple crawling legs.
- 2. The appearance of these limbs (represented as perfectly disengaged in Mr. Thompson's Plate II. fig. 11.) previous to the shedding of the cephalothoracic shield and anterior parts of the body, is totally at variance with the principles of ecdysis observable throughout the *Annulosa*, in which the locomotive organs, at least the legs, are the last which are disengaged, and the thoracic shield of the inclosed animal the first portion exposed to view. It would, in fact, be impossible for the Zoe to disengage the thoracic limbs without the thorax itself being previously withdrawn from its covering.
- 3. But we will look more precisely at the nature of this supposed disengagement of the five pairs of legs. This, in the absence of any precise explanation given by Mr. Thompson, may be presumed to be effected in three different ways.

Firstly,—as indeed Mr. Thompson appears to suppose by his statement that the large natatory limbs "become" simple ones,—this may be effected by the two pairs of large natatory limbs entirely throwing away their outer covering, whereby the five pairs of small simple legs, which had been previously inclosed within them, are disengaged. This I take to be the true nature of the disengagement of the organs of motion in the Annulosa; but if we regard this to take place in Zoea, we shall necessarily have two conditions totally at variance with the principles of ecdysis, viz. that an existing organ in a state of incomplete development incloses only a single organ,—thus, the wings of the Grasshopper are not inclosed within the legs of its larva; and that an organ disengaged by the shedding of its envelope is always larger than such envelope. This, in fact, is the very end of the metamorphoses of the annulose animals, the hardness of their outer covering preventing their growth, except by the shedding of such covering.

Secondly, We may imagine that the five pairs of minute rudimental legs of the future Crab are not transformed from the two pairs of natatory limbs, but are totally

unconnected with them, being, as Mr. Thompson himself says, "disengaged from beneath the clypeus", (and his Plate II. fig. 2. represents the same idea,) and having no previous existence in the young Zoe. Now if this be the case, setting aside its disagreement with the recognised conditions of development, we arrive at once at this startling and important conclusion, namely, that the large natatory organs of the Zoe are instrumenta cibaria, foot-jaws, in fact, and that the animal in its Zoe state has no true legs. Without, however, asserting (which might reasonably be done) that every annulose animal which in its immature state is furnished with locomotive organs, is also furnished with instrumenta cibaria, which latter legitimately represent the instrumenta cibaria of the imago, whilst the former as truly represent the true legs of the imago, we may assert, that where an immature annulose animal is furnished with locomotive organs, these, or at least some of them, represent the true thoracic legs of the imago, and are not, in such immature state, merely rudimental trophi of the perfect animal. Now on applying this principle to the case in question, we find the Zoe furnished both with trophi and natatory organs; and if we regard the trophi, although few in number, as representatives of the trophi, and the two pairs of natatory organs as representatives of the locomotive organs of the future Crab, we can only regard the five pairs of disengaged limbs either as representing the subabdominal appendages of the Crab, or as simple thoracic appendages (distinct from legs), or as supplemental limbs. But each of these suppositions is so contrary to nature with reference to the organization of Zoe or the Crab as distinct animals, that in order to show their futility it will be sufficient to notice the determinate leglike form of these disengaged limbs, the first pair of which is cheliferous; the fact that the Zoea has distinct subabdominal appendages; that the Crustacea are not, like the Myriapoda, furnished with auxiliary limbs; and that true thoracic locomotive organs (which in Zoe, according to the principles above stated, must still remain undeveloped,) are constantly developed at the same time as, or even before, supplemental ones.

Thirdly, We may imagine the disengagement of these "future limbs" to take place in a mixed manner, by considering that the two pairs of natatory limbs of the Zoe produce the first, or chelate, and second pairs of legs, and that the three posterior pairs are simply disengaged from beneath the clypeus. Against this idea many of the preceding observations may be conjointly adduced; to which it may be added, that the similar size of these disengaged limbs is sufficient to prove that they must have undergone an equal degree of development. Moreover, in such case the chelate members, which are larger than the following limbs, must be produced from the first pair of natatory limbs of the Zoe, which are much smaller than the second pair.

I have in these observations left unnoticed the small member anterior to the claws, observed by Mr. Thompson, and considered by him as the rudiment of the outer footjaw, which offers still greater difficulties as to its nature if we adopt Mr. Thompson's views, but which, as I shall subsequently show, is a necessary organ of the Zoe.

- 4. In the next place it is to be observed, that Mr. Thompson's figures and statements relative to the gradual development of the Zoes are totally at variance with one of the received principles of ecdysis, which may be thus stated. When an animal undergoes a variety of moultings, attended by alteration in form or development of organs, there is a gradual tendency towards the organization of the perfect animal. Now Mr. Thompson expressly states that his large Zoes differed from the smaller ones in the greater degree of development of all their organs. This therefore is precisely what would occur in case the large Zoes were perfect animals; and it is precisely what would not take place if the subsequent state of the Zoe were a Crab.
- 5. It is worthy of notice that there are several peculiarities in Zoea so evidently partaking of the Macrourous type, that it is surprising that Mr. Thompson should not have noticed that these characters present themselves in so complete a state of development, when compared with the Macroura, as to negative the opinion that these animals would ever become Brachyurous. The elongated tail, the rostrated cephalothorax, but more especially the structure of the mandibles and two pairs of maxillæ, may especially be noticed.
- 6. If, as we shall subsequently perceive, there be no pretence for doubting the correctness of Rathke's researches upon the Cray-fish, which is clearly proved to undergo no metamorphosis, I think we are fully warranted from analogy in considering that the other Decapods do not undergo metamorphosis. Mr. Thompson, indeed, seems inclined to consider that in such case the Cray-fish "can only be regarded as one solitary exception to the generality of metamorphosis*;" although he had previously given his opinion of the weight of analogy in the second number of his Researches, by stating that "metamorphosis having been proved in a single instance amongst animals so uniform in structure as the Homobranchia, we may safely infer from analogy, as far as regards the particular tribe alluded to, that it is general."

These six considerations induce me to adopt the opinion that no sufficient ground has been shown by Mr. Thompson for supposing that a metamorphosis of Zoes into Crabs takes place.

Secondly, therefore, we will proceed to notice Mr. Thompson's statements relative to the hatching of the young Zoes from a female of the common Crab, and which he states took place under his own eye. It is much to be regretted that Mr. Thompson, having such ample opportunity, did not dissect the ova in various states, so as to ascertain in the most satisfactory manner the gradual development of the embryo, as Rathke has done in the Cray-fish. The statement, although short, has, however, such sufficient precision, that we are compelled to believe either that (notwithstanding whatever may be advanced to the contrary) the young of the common Crab are Zoes, or that the latter are parasitic animals, which in some unexplained manner are introduced in the embryo state beneath the abdomen of the Crab; and if we consider the large Zoes observed by Mr. Thompson to be perfect animals, there is some ground

for the latter opinion in their comparatively less perfect organization, a circumstance to which a completely analogous case exists amongst the *Hyperiidæ* in the order *Amphipoda*, &c. Zoe, indeed, is not the only animal respecting which this kind of parasitic obscurity exists; the genus *Meloe* amongst the coleopterous insects is perfectly analogous, the young of which, according to some authors, are *Acari*, whilst others state them to resemble the perfect insect. I am the more anxious to offer this explanation of Mr. Thompson's argument, in as much as the facts subsequently stated respecting the ova and young of the *Brachyura* are totally at variance with Mr. Thompson's assertions.

Thirdly, As respects Mr. Thompson's statements relative to the young of the common Lobster, we have again to regret the slightness of the information given to us upon this branch of the subject. The young is called a modified Zoe, a cheliferous Schizopode, with a frontal spine, a spatulate tail, and wanting subabdominal fins, undergoing a metamorphosis less in degree than the other mentioned genera. We are left in uncertainty whether there are eight pairs of locomotive organs, as in the true Schizopods, or whether these organs are all divided into two parts; the only evidence of such Schizopod nature being the chelate limb figured; and yet this is precisely where information was required. Examine the other characters given of this "modified Zoe" without reference to its undescribed legs, and we are able to trace (notwithstanding Mr. Thompson's assertion to the contrary) precisely such an animal as might be expected for an immature Lobster. But if we examine the nature of the cheliferous member figured, we shall find the strongest reason for considering that this "larva" is not a Schizopode. Fig. a. represents the cheliferous member of the perfect Lobster, as well as of its larva; but this organ is not provided in the perfect state with any lateral appendage. And Mr. Thompson himself does not attempt to prove the connexion of the lateral appendage which he figures with the cheliferous limb of the perfect Lobster, since he describes this lateral appendage as the future flagrum of the Lobster, that is, the lateral division of the exterior pair of foot-jaws; consequently, unless Mr. Thompson is prepared to prove that the lateral appendage of one organ in the immature state becomes the lateral appendage of a totally distinct organ in the perfect state of the same animal, it must follow that this gentleman has erred in his dissections of the immature Lobster, and mistaken the lateral appendage of the outer foot-jaw for a Schizopodous appendage of the Cheliferous limb.

Fourthly, As respects the explanation or "excuse" which this principle of metamorphosis enables us to give for the annual migrations of the land Crabs of the West Indies to the ocean to deposit their spawn, the young produced from which being natatory animals—Zoes, in fact,—are incapable of living in the same element as their parents in their early stages, I can very well agree with Mr. Thompson that if any exception existed amongst the *Crustacea*, in which the young should not undergo any change from aquatic to terrestrial habits, accompanied of course by a

corresponding modification of structure, it would be amongst the land Crabs; but I cannot agree with this gentleman that scarcely a stronger confirmation than this very circumstance could be adduced of the universality of metamorphosis, in as much as it appears to me that Mr. Thompson has arrived somewhat too suddenly at the conclusion that the young must consequently be Zoes, or even that, although incapable of living out of the water, they are necessarily furnished with natatory members. Examine the sea Crab, and no material difference in the structure of its locomotive organs is to be observed from that of the land Crab whence a different kind of motion can be inferred; hence there can be no actual necessity for the existence of natatory apparatus in the young land Crab, which must be just as able to support itself in the water without any such as an ordinary sea Crab. If, moreover, we examine the structure of the branchial apparatus of the land Crabs, we find still further evidence in support of this argument. MM. Audouin and M. H. Edwards, in the Annales des Sciences Naturelles for September 1828, have given an account of this organization: the exterior of the branchial cavity is furnished with a reservoir for containing a supply of water; and in the land Crab there is moreover a second vessel destined for the like purpose, whence it is evident that in this respect the land Crabs do not materially differ from the sea Crabs. I will not dwell upon this subject further than to refer to the conclusive facts subsequently stated in proof that the young of the land Crabs is neither a Zoe nor furnished with natatory apparatus.

Fifthly, I will only observe with reference to Mr. Thompson's general assertions, that no great weight ought to be attached to them until the necessary details shall have been given to the public, more especially if, as I have shown to be the case, we find cause in those already published to distrust the views of the author.

Having thus gone through the various statements made by Mr. Thompson in support of his theory, and ascertained from them the apparent want of confirmation of such theory, I proceed to notice the opinions of crustaceologists whose writings have established for them some degree of weight as authorities upon the question.

These observations will be confined, firstly, to such as bear directly upon Mr. Thompson's statements, and secondly, to such as relate to facts noticed respecting the transformations in the early stages of various animals in the class; since it is the more necessary in endeavouring to ascertain the correctness of the views of an author, to reject all general assertions made by others to the contrary which have not been made in reference to such opinion, or which do not rest upon direct observation. And it is to be regretted that Mr. Thompson's memoirs have been far from generally known; this will account for the slight degree of attention which has been bestowed upon the interesting subject upon which they treat, and for the paucity of notices respecting them.

We find Latreille*, however, stating that the opinion of Mr. Thompson "a grand besoin d'être étayée par des expériences positives, si toutefois elle n'est pas erronée."

^{*} Cours d'Entomologie, p. 385.

M. Edwards, the most celebrated of modern living crustaceologists, observes, that as the *Malacostraca Podophthalma* are divisible from the presence or absence of branchiæ to the thorax, inclosed in a peculiar cavity, "on n'aura plus d'incertitude sur la place que doit occuper un genre très curieux, Zoea; en effet, un examen attentif de ces petits animaux m'a convainçu que non seulement leurs yeux sont portés sur des péduncles, mais aussi de chaque côté de leur thorax il existe sous le carapace une cavité respiratoire renfermant des branchies semblables par leur structure et leur position à celles d'autres Macroures. Il est donc evident pour moi que le Zoe est réellement un Crustace de l'ordre des Décapodes. Mr. Thompson assure que cet animal n'est autre chose que le jeune de Crabe commun. Cette opinion me ne paraît pas soutenable, mais neanmoins il serait possible que les Zoes observés jusqu'ici ne soient pas des animaux adultes, et alors il se pourrait bien que par les progrès de l'âge ils deviennent assez semblables aux Megalops; question que nous nous proposons de traiter plus au long dans une autre occasion*."

The talented editor of the Zoological Journal has also, in his review of Mr. Thompson's work, expressed his doubts as to the universality of the fact of metamorphosis taking place in the *Crustacea*; and in the eighteenth number of that work he has stated the confirmation which his doubts had received by the publication of Dr. Rathke's work, adding, that if there existed no optical delusion or other cause of error in the isolated observations which Mr. Thompson has given us, the difference of organization between a Macrourous and a Brachyurous Decapod is much greater than either analogy or anatomy would have led him to suspect.

And lastly, Mr. Kirby has communicated to me his conviction that the researches of Mr. Thompson are to be regarded with distrust, the grounds for which opinion will appear in his forthcoming Bridgewater Treatise.

I now proceed to notice, as concisely as possible, the direct observations made by various authors upon different Crustaceous animals in the young state.

And in the foremost place are to be mentioned the elaborate researches of Rathke upon the development of the ova of the common Cray-fish, a work which for minute and delicate investigation is rivalled only by Lyonnet's celebrated memoir upon the larva of Cossus. Some idea may be entertained of the extent of these inquiries, from the fact that five large folio plates are completely filled with details of the structure, internal and external, of the ova in various states of development, and of the newly hatched animal. And so beautifully clear are the representations of these objects, and so completely is the development of the embryo to be traced through all its stages, that unless we believe the whole to be the work of a fanciful imagination, it is impossible to arrive at any other conclusion than that the Cray-fish does not undergo any change which can in the least degree merit the name of metamorphosis. A full abstract of this valuable memoir is inserted in the eighteenth number of the Zoological Journal, and in the Annales des Sciences Naturelles for August 1831,

the latter of which is accompanied by four plates. I will therefore content myself with referring the student to these accessible sources, without attempting to give even an outline of the elaborate investigations in question.

LATREILLE, speaking of the young of the Cray-fish, says: "Les jeunes écrevisses, très molles au moment de leur naissance, et toute-à-fait semblables à leurs mères, se réfugient sous leur queue, et y restent pendant plusieurs jours et jusqu'à ce que les parties de leurs corps soient raffermies *."

Mr. Thompson himself, in the genus *Mysis*, has clearly shown that these animals, which he has proved to be most intimately allied to the Decapod *Macroura*, undergo a series of changes, which he states "cannot be considered as metamorphoses, but simply a gradual development of parts †."

The above appear to be all the direct observations hitherto made upon the *Podoph-thalma* (with the exception of those subsequently detailed from my own researches); but amongst the sessile-eyed *Malacostraca* we have more numerous observations.

Of these, as in the former, the researches of RATHKE again stand foremost; since, in a series of memoirs, very recently published, upon the development of the ova and embryos of various animals, we find the common Asellus aquaticus to have been investigated by him, with the result that no material alteration takes place in the form of the animal ‡.

In the Annales des Sciences Naturelles for December 1833, is published a valuable report, by M. Isidore Geoffroy St. Hilaire, upon a memoir of M. H. Milne EDWARDS, entitled "Observations sur les changemens de forme que les Crustacés éprouvent dans le jeune âge." Passing over the more generalized views deduced by M. St. Hilaire from the facts noticed by M. Edwards, I shall merely state the latter. The genus Cymothoa, and some other Isopodous genera, afforded to M. Edwards an easy opportunity of examining the development of the eggs and the structure of the young, in consequence of their being inclosed within the large subthoracic pouch. Hence he was enabled to ascertain that some organs which are fully developed in the adult animal, are either rudimental or absolutely wanting in the early state: thus, in the latter the animal has only six thoracic segments, and six pairs of legs, although when adult it has seven segments and seven pairs of legs. On the contrary, other organs, which are fully developed in the young, become rudimental in the adult state: thus, in the former we find a large head, furnished with two large oval black eyes, and the abdominal segments nearly as large as the thoracic ones; whilst in the adult state the head is extremely small, the eyes are not externally visible, and the abdominal segments are very short and linear. M. Edwards has also made similar observations upon many other genera, especially upon Anilocra, in which a pair of legs is also developed after birth (the same likewise takes place in

^{*} Règne Animal, tom. iv. p. 90. 2nd edit. † Zoological Researches, p. 16.

[‡] Abhandlungen zur Bildungs ant Entwickelung-geschichte des Menschen und der Thiere. 4to. 2 parts. 1832, 1833.

Oniscus, as De Geer long ago remarked); upon Cyamus, a genus of Læmodipoda, which in the young state is of a slender and cylindric form, but which afterwards becomes much enlarged and depressed; also upon Phronyma, a genus of Amphipoda, remarkable for its large head, conical thorax, and singular construction of the fifth pair of thoracic legs, but which in the young state exhibits a head of ordinary size, a thorax larger in the centre than at the extremities, and the fifth pair of legs not unlike the others, and not didactyle.

From the modification in form which the existent organs undergo in the passage to the adult state, M. Edwards deduces this curious theory,—that the changes of form which the Malacostraca undergo constantly tend to remove the animal to a greater distance from the type which is common to the greatest number of individuals in the group, so as to individualize it more and more completely. Thus the form of the immature Cymothoa or Phronyma, for instance, is referrible to the general typical form of the Isopoda or Amphipoda; but, by the gradual change of form, these animals are exhibited in forms the furthest removed from the types of their respective orders.

It is evident, however, from these remarks, that the *Edriophthalma* undergo no change worthy of the name of metamorphosis; and this is most fully supported by the observations of Latreille upon the *Isopoda* in general, viz. that the progeny "naissent avec la forme et les parties propres à leur espèce, et ne font que changes de peau en grandissant*"; of Mr. Montague upon *Caprella Phasma*, who states that he observed ten young ones crawl from the abdominal pouch of the female, "all perfectly formed" ; of Mr. Coldstream in an admirable paper upon *Limnoria terebrans*, inserted in the Edinburgh New Philosophical Journal of Professor Jameson for April 1834; and, lastly, of Professor Zencker in his memoir "De Gammari Pulicis Historia Naturali," 4to, 1832.

Hitherto I have confined these observations to the *Malacostraca*, because it is in that division of the class that the non-existence of metamorphoses has been denied. The *Entomostraca* are admitted on all hands to undergo very material modifications of form, as may be seen from the researches of Jurine, Strauss, Prevost, &c.; whilst Mr. Thompson's recent memoir upon *Artemia* (not *Artemis*,) is an additional evidence of the same fact, although the nature of the various alterations is very far from being detailed in that satisfactory manner which the author seems so capable of doing.

I have therefore now to detail, as the third portion of this essay, such circumstances as have fallen under my own observation relative to this interesting inquiry, the tendency of which is precisely similar to that exhibited by the two preceding portions of my treatise.

We have seen that Mr. Thompson's chief argument is founded upon the supposed transformations of the Zoe into a Crab. His Zoe, figured as the just-hatched larva of the common Crab, is not so large as a large pin's head. Slabber's "changed Zoe" is represented as three lines long; and Mr. Thompson's Zoe, which died on the sup-

^{*} Règne Animal, tom. iv. p. 131.

posed point of transformation into a Crab, is nearly four lines long between the tips of the spines. Now if Mr. Thompson's views be correct, and these latter Zoes are to be regarded as the larvæ of Crabs, they must be considered as having acquired the maximum of their Zoe form; but so far is this from being the case, that I have obtained from the collection of the late Rev. Lansdown Guilding, specimens of a species of Zoea ten lines long between the points of the spines; a size far too large to allow us to suppose that they would subsequently put off their Zoe form, and appear as Crabs; bearing at the same time in mind the minute size of the latter animals in the very young state, although possessing their ordinary form.

Of this West Indian species I have given, in the accompanying sketch, figures in detail of the various organs, which I shall not describe at length. The palpigerous mandibles, the two pairs of antennæ, one pair of which is bipartite, the multilobed inner maxillæ, are all characters found in the Macroura and Schizopoda, but not in the Brachyura. The natatory apparatus of the tail, observed in my species and unnoticed by Mr. Thompson, is also similarly characteristic, but the locomotive organs are those to which the highest importance attaches with respect to the real nature of the animal. At first sight, in addition to and immediately succeeding the two pairs of maxillæ, there appear only two pairs of large locomotive bipartite organs. These therefore, on the supposition that the Zoe is the young of a Decapod animal, must either be legs, or outer foot-jaws greatly developed; and from their bipartite structure, the latter may be partly assumed; but upon carefully dissecting the animal, a series of organs were found, which not only fully proved this to be the case, but also led at once to the discovery of the real nature of these animals, and gave a clue for the correction of Mr. Thompson's ideas upon the supposed disengagement of the thoracic limbs. Immediately succeeding the outer pair of the natatory organs, and, in fact, lying between them when at rest, was discovered a pair of slender minute organs, composed apparently of two joints, one long and one short, and furnished at the base with a still more minute lateral appendage. Beyond these, in succession, were found the five pairs of organs precisely similar to Mr. Thompson's "limbs of the future Crab disengaged from beneath the clypeus." Moreover, a number (undetermined) of minute fleshy elongated masses were found near and attached to the base of these limbs. Are we therefore, with Mr. Thompson, to suppose that in this Zoe (and all the specimens were alike) metamorphosis had commenced, whilst not the slightest trace of such a process could be observed beyond this acquisition of rudimental limbs, which can otherwise be much more satisfactorily accounted for? The researches of recent authors, and those particularly of M. H. MILNE EDWARDS, have clearly proved that in some species of Decapods (Acetes, Sergestes,) one or more pairs of legs become rudimental, and that their place is supplied by highly developed foot-jaws.

Now upon applying this theory, to the correctness of which Mr. Thompson bears witness, to Zoea, we find that the two large pairs of natatory organs represent the

first and second pairs of foot-jaws of the typical Decapods immensely developed; the minute pair of organs following these to be the third pair of foot-jaws; the five pairs of "limbs of the future Crab" to be the real thoracic legs of the Zoe, and that the minute fleshy masses are evidently branchiæ. Thus we perceive that the possession of these limbs, instead of being an evidence of the imperfect state of the Zoe, is a proof of its anomalous perfection; and thus we arrive at the unexpected conclusion that Zoea is a genus of Decapod Crustacea, for the reception of which amongst the Macroura a distinct section must be established.

With reference to Mr. Thompson's statements respecting the hatching of the Zoes from the eggs of the common Crab, and the arguments adduced from the habits of the West Indian land Crabs, I am able to offer the following as, I trust, very conclusive observations to the contrary.

In the collection above alluded to were contained, in spirits, the abdomens of several female Crabs, having the interior surface covered with hundreds of eggs or newly hatched young. One of the bottles in which one of these was deposited was labelled by Mr. Guilding, "Eggs and young of a land Crab not undergoing a metamorphosis." From this specimen I obtained eggs, and young Crabs evidently just hatched, and others at a rather later stage of their growth.

The eggs are of a dark reddish colour, showing through the outer integument the rudimental limbs of a future animal of a paler colour. On removing the thin transparent pellicle which surrounded one of these eggs, the eyes of the future animal were most conspicuous, the tail was seen extended as a narrow plate, nearly reaching to the eyes, and along its sides lay the large anterior cheliferous and the four following simple pairs of limbs. The existing organs, although perfectly discernible, occupied only a small portion of one side of the egg, its greater part being filled with hardened matter composed of minute molecular grains. The animal was in a sufficiently forward state of development not to allow the least doubt to be entertained as to the nature of these limbs, nor did any organs appear answering to the two large split pairs of natatory organs of Zoea. The branchiæ, in a fleshy and unorganized state, were also found at the base of the legs. The eggs are $1\frac{1}{2}$ line in diameter.

In the accompanying sketches I have represented one of the Crabs evidently just

In the accompanying sketches I have represented one of the Crabs evidently just hatched, being about $1\frac{3}{4}$ line long, and having the upper part of the cephalothorax considerably swollen. From my figures, the very rudimental state of the two pairs of antennæ, and of the feelers or flagrums of the outer foot-jaws, will be perceived; but the general form of the animal is thus early exhibited, and the developed state of its branchiæ and the want of subabdominal appendages are especially noticeable. In the following sketch the animal is seen in a somewhat more advanced stage of its growth, being rather more than 2 lines long, and in which the upper surface of the cephalothorax has acquired its ordinary shape, and the antennæ have attained a greater degree of perfection.

These circumstances are, I trust, amply sufficient to prove that the land Crab does not undergo any metamorphosis.

It is to be observed that Mr. Guilding has not stated the precise species of land Crab of which the above-mentioned individuals were the offspring; but his well-known acquirements in crustaceology put the question of its being at all events a species of land Crab to rest. Should this, however, be nevertheless called in question, the argument which I would deduce from it will be but little diminished even were it a sea Crab.

We have seen that Mr. Thompson's supposed full-grown Zoe, which died on the point of undergoing its supposed metamorphosis, was 3 lines long between the points of the spines, and the length of which, from the head to the tail, must have been at least $1\frac{1}{2}$ line. But the young of the common Crab is found of a much smaller size than this, exhibiting at the same time all the form of the full-grown Crab. I have myself captured the young of *Cancer Mænas* not more than $\frac{1}{2}$ a line long, yet perfectly formed, and capable of running about with much quickness.

Although disagreeing with Mr. Thompson in respect to his theory, I have already stated that his figures are very faithful delineations of nature. I have therefore the more pleasure in stating that his representations of the young of *Mysis* are (as I have ascertained by extracting them from the subthoracic pouch of the female) correct.

Hence, by taking the preceding observations into consideration, we find that one or more types of each of the great groups of the typical Malacostracous *Crustacea* have been ascertained to undergo no change of form sufficiently marked to warrant the employment of the term metamorphosis. Thus,

The Brachyura are represented by the Land Crab.
The Macroura — Cray-fish.
The Schizopoda — Mysis.
The Amphipoda — Gammarus and Phronyma.
The Læmodipoda — Caprella and Cyamus.
The Isopoda — Asellus, Cymothoa, and Limnoria.

Note.—Since the preceding pages were written, Mr. Thompson has published a memoir upon the genus *Pinnotheres*, belonging to the *Brachyura*, in which the ova are stated to have been seen to hatch in great numbers under the form of a new kind of Zoe, without the circumstances attending their development being recorded. And, on the other hand, some of the late Mr. Guilding's MSS. have been published in the Magazine of Natural History, in which it is distinctly stated that the land Crabs do not undergo transformations.

Explanation of the Plate.

PLATE IV. A.

- Fig. 1. Zoea Gigas, Westw. natural size.
- Fig. 2. Ditto, magnified.
- Fig. 3. The outer antenna.
- Fig. 4. The inner antenna.
- Fig. 5. The labrum.
- Fig. 6. One of the mandibles, a representative of the the palpus.
- Fig. 7. One of the interior maxillæ.
- Fig. 8. One of the second pair of maxillæ.
- Fig. 9. One of the first pair of foot-jaws, developed into a natatory organ.
- Fig. 10. One of the second pair of foot-jaws, developed into a natatory organ.
- Fig. 11. One of the third pair of foot-jaws, minute and rudimental.
- Fig. 12. View of the underside of the body, as extracted from the cephalothoracic shield.
 - a. The first pair of foot-jaws.
 - b. The second pair.
 - c. The third pair.
 - d. The anterior pair of chelate members.
 - e. The rudimental branchiæ.
 - f. The four posterior pairs of simple members.
- Fig. 13. One of the subabdominal appendages.
- Fig. 14. The tail, developed.

PLATE IV. B.

- " Eggs and young of a land Crab not undergoing a metamorphosis."—Guilding, MSS.
 - a. The egg.
 - Fig. 1. Natural size.
 - Fig. 2. Magnified, seen in front.
 - Fig. 3. The same, seen in front, having the outer pellicle stripped off: the legs on one side extended laterally, the branchiæ visible on the other side.
 - Fig. 4. The same, seen in front, having the outer pellicle stripped off, seen sideways.
 - Fig. 5. The same, seen in front, having the outer pellicle stripped off, seen sideways, with the limbs and tail extended.
 - Fig. 6. The tail.
 - Fig. 7. The legs, with the branchiæ at the base, not organized.

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- b. The young in its earliest state.
- Fig. 8. Natural size.
- Fig. 9. Magnified.
- Fig. 10. Ditto, seen from beneath.
- Fig. 11. Anterior portion of the body, from beneath, showing the outer foot-jaws, two pairs of antennæ, and eyes at the extremity of the peduncles.
- Fig. 12 & 13. One of the rudimental internal antennæ attached to a large fleshy tubercle.
- Fig. 14. One of the rudimental external antennæ.
- Fig. 15. One of the outer foot-jaws.
- Fig. 16. One of the intermediate foot-jaws.
- Fig. 17. The branchiæ.
- Fig. 18. The abdomen, unfurnished with internal appendages.
 - c. The young at a rather more advanced period.
- Fig. 19. Natural size.
- Fig. 20. Magnified.
- Fig. 21. The anterior part of the body seen from beneath.
- Fig. 22. One of the internal antennæ separated from its large basal lobe.
- Fig. 23. One of the external antennæ.
- Fig. 24. The abdomen.