

XXVIII. *On the Development of Decapod Crustacea.* By C. SPENCE BATE, F.L.S., &c.
 Communicated by Sir W. SNOW HARRIS, F.R.S.

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MANY years have elapsed since Mr. VAUGHAN THOMSON made the important discovery that the *Zoëa* of naturalists was but the immature form of an adult Decapod.

His fortunate observation was received with the greatest caution by zoologists in general, and several undertook researches upon the subject to demonstrate the error into which they assumed he had fallen. The researches of RATHKE upon the *Astacus fluviatilis*, of MM. MILNE-EDWARDS and AUDOUIN upon marine Decapoda, together with those of Mr. WESTWOOD upon the genus *Gegarcinus*, for a considerable period delayed the general acceptance of the fact that the *Zoëa* is the larva of a Decapod.

RATHKE, in 1840*, published the results of a second investigation on the subject, being his researches upon *Pagurus*, *Astacus marinus*, and *Hyas*. In these he corroborated the statements of Mr. THOMSON, and admitted that, “relying on the history of the development of the Crayfish, and trusting too much to analogies in the structure of full-grown Decapods,” he had done Mr. THOMSON injustice in not putting faith in his discovery.

It was not long after Mr. THOMSON’S first valuable discovery that good fortune placed within his reach the opportunity to show some other changes that the young animal passed through in its transition to a perfect creature; and by a singular coincidence, the same volume of the Philosophical Transactions which contains Mr. WESTWOOD’S refutation of what he calls Mr. THOMSON’S theory, also contains that latter gentleman’S further discoveries of what has been termed the metamorphoses through which the animal passed in its growth to the mature Crab; and where he demonstrates that the *Zoëa* and *Megalopa* of naturalists are but two forms in the development of one and the same animal. Mr. COUCH, Mr. GOODSIR, M. JOLY, Captain DU CANE, RATHKE, BELL, and most naturalists have since confirmed the assertion of Mr. THOMSON, and affirm that two remarkable metamorphoses take place during the progressive development to the adult stage. This is accepted as the present state of our knowledge in Dr. CARPENTER’S recent work on the microscope, and in Professor BELL’S ‘British Crustacea.’

To this general rule a few exceptions exist. The Land-crabs and freshwater Crayfish form the most important. Beyond these we know of none in the same orders of Crustacea, the young of which quits the ovum with all its members developed and closely approximating in form to that of the adult.

* Annals of Natural History, vol. vi.

This is the case with all the Edriophthalma; and in the Report upon the British Species which I was requested to lay before the Members of the British Association, the following passage occurs:—"In the highest types of Crustacea, the immense variety of change from the *Zoëa* to the adult animal is but the result of *subordinate* becoming *more important* parts, together with the development of others not yet present, and therefore hardly acceptable under the signification of metamorphosis*."

It is this opinion that I am now, to the best of my ability, about to demonstrate, that from the *Zoëa* or larval form to that of the well-developed Decapod, there is no sudden change such as is understood by the term metamorphosis, and generally believed by naturalists; but that the development is gradually progressive throughout; that some parts are absent, and that some which are present may become obsolete, but that each part undergoes gradual transformation.

In order to arrive at a degree of certainty, the researches upon this subject have been confined to one species, others being used as collateral evidence only. The larvæ in the earliest stages were procured direct from *Carcinus Mænas*, being hatched in my own possession. Those of a later period have been the result of two or three years' accumulations, most of which were taken in Plymouth Sound. Thus procuring a number, I have been enabled to trace through a scarcely broken chain the progressive development of the respective parts up to that which they assume in the adult animal.

The embryo, when it first quits the egg (Plate XL. fig. A), is enclosed within a general tunic, which embraces each individual member and is conformable to the whole animal. This tunic is of extreme tenuity and exceedingly transparent; it is very liable to be overlooked without close observation. Within this tunic may be distinctly seen the hairs belonging to each part respectively. These are not extended, but retracted with telescopic joints, within the members of which they form appendages. In this way also the larger processes of the caudal extremity (fig. 21') are contracted within shorter limits, as are also the horn-like processes upon the dorsal surface and frontal region. These two are moreover folded down, the dorsal laid forward upon the top of the head, the frontal brought down between the eyes and compressed beneath the frontal region (fig. A). In this embryonic condition the animal swims about for a few hours. It then liberates itself from the general tunic by throwing off that portion which covered the head and *pereion*, anteriorly, while that which protects the *pleon* is drawn off posteriorly †.

The animal is now freed from its embryonic condition, and more actively sports in the water, and procures its own food. Its gambols are produced, partly by the action

* The author is perfectly aware that in Insecta the change of the animal within the chrysalis is gradual in development; but he wishes to show that there is no stage in Crustacea answering to the chrysalis; that the moults in process of development of the Crustacea are of the same kind as those which take place in the adult condition.

† The terms used in this paper are those suggested by the author in his Report on the British Edriophthalma (British Association Report for 1855, p. 27), instead of the old and incorrect synonyms of Thorax, Abdomen, &c. The accompanying diagram of an imaginary *Zoëa* exhibits the details in position.

The term *pereion* is derived from *περαιώω*, to walk about, being that portion of the animal which supports

of the entire *pleon*, and partly by the gnathopoda, the (so-called) natatory feet. They together induce a jerking motion in a progressively circuitous course.

In this stage I have carefully and extensively examined every part of the animal both in position and in detail.

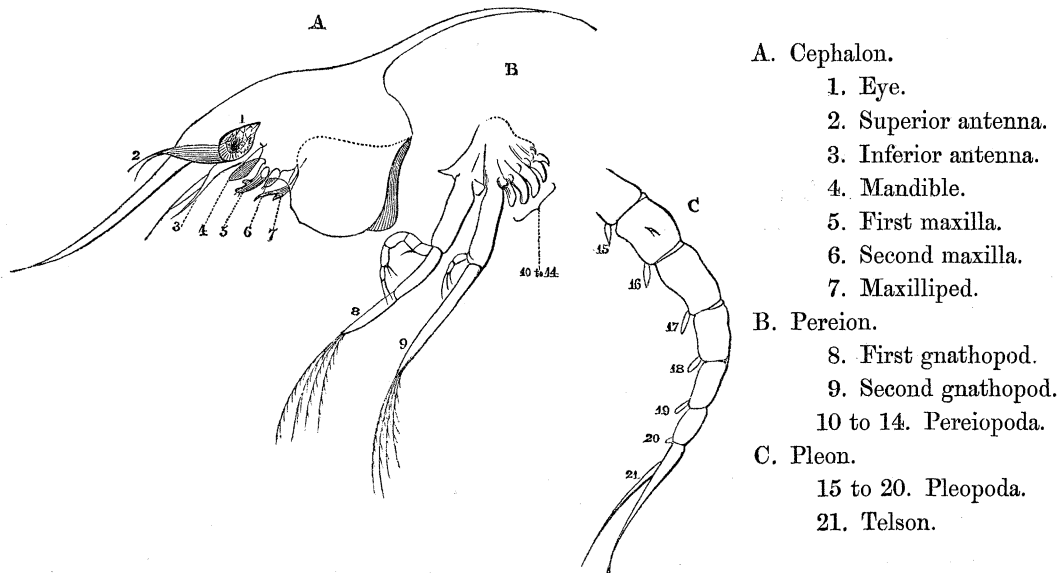
The *carapax* covers almost the whole of the *pereiion*, and extends in front to a long projecting rostrum, which is nearly half the length of the entire animal. A similar projection arises from the centre of the dorsal region, and gives an increased eccentricity to its general appearance—a circumstance which has lent considerable force to the belief of an exaggerated metamorphosis in the history of the development of the Crab.

In this early stage the dorsal spine is no mere ornament, but possesses a specific use in supporting the heart in its position. We thus are enabled to identify its exact position in the homologies of the adult, with the cardiac region on the carapax, which in some genera are actually represented by a stout spinous protuberance. It appears moreover to be analogous in purpose to the two strong processes found upon the internal surface of the same region of the carapax in *Carcinus* and other genera.

Posteriorly, as in the adult animal, the carapax is centrally attached to the *pleon* by a membrane, while on each side it is free, so as to admit even at this early period an inpouring current of water to aërate the branchiæ. Laterally the carapax overhangs the *pereiion* and protects the coxæ of the developed members, but anteriorly it is compressed so as to leave the eyes prominent.

In the early form the eye is generally considered by naturalists to be sessile; and if our observations were to be confined to certain *Macroura*, it would be difficult to disprove the assertion, since the distinction between eyes that are supported upon almost obsolete peduncles and those which have none is very limited.

the walking legs: hence *pereiopoda*. *Pleon* is taken from πλέω, to navigate, being that part of the animal which supports the limbs by which it swims about: hence *pleopoda*, the swimming feet.



But in the larva of the *Brachyura* that we are now describing, the carapax is seen to pass distinctly round the base of the eye and the peduncle to be continued beneath the carapax, as in fig. B', Plate XL. and fig. 1, B, Plate XLVI., and thus demonstrates the podophthalmic character of the larva even in this early stage.

The pair of appendages (Plate XL. figs. A and B, 2) first succeeding the eyes represent the anterior or upper antennæ. They respectively consist of a single articulation, narrowing towards the extremity, where are planted two short simple hairs, and two long almost invisible ones of the character that I have elsewhere* termed auditory cilia, since they are only found to exist upon the antennæ which support the acoustic organs. This fact enables us immediately to identify this immature appendage with the perfected structure, even at the earliest commencement of the young creature's life; and also demonstrates that the germ or rudiment of the filament, on which part only the auditory cilia are ever found, is present.

The second pair of appendages (Plate XL. fig. A and B, 3) represent the second or inferior antennæ, each of which in this stage consists of a basal articulation supporting a finely serrated spine, which is in fact a process of the same; and a flat, long, and squamiform articulation, ornamented at the extremity with two simple hairs, one longer than the other. At the base of these two appendages may be distinguished a small papilla—the germ of the future antenna (3 a).

The next succeeding pair of members are the mandibles (Plate XL. fig. B, 4). These differ from the adult organs in the absence of the appendage and the internal lever processes. In general form they manifest a striking approach in their present immature condition to those of *Talitrus* among Amphipoda (Plate XLVI. fig. 4 Q).

Posterior to these succeed the first pair of maxillæ (Plate XL. fig. B, 5), which consist of three squamiform plates, corresponding with those found in the adult, each capped with ciliated hairs, numbering about five or six upon the central or larger plate. These are stouter than on the other two, and approximate with increasing age more and more to the character of spines. They also increase in number.

The *second* pair of maxillæ (Plate XL. fig. B, 6) succeed immediately in position to the first, and in the earliest stage are developed upon the type of those of the adult. Each of them consists of three squamiform plates, equally divided at the apex, and fringed with plumose cilia. The plates are more uniformly equal than in the adult. At the base, the plate which homologizes with the flabella and branchia is present, and developed into a form that differs somewhat from, but probably fulfils the purpose of, an outletting valve at the anterior extremity of the branchial chamber, similar to the same organ in the adult.

The next succeeding pair of appendages should homologize with the maxillipeds, but these appear not to be present in this early form; and those which do follow are evidently, even at the present period, the immature form of the first pair of *gnathopoda* (Plate XL. figs. A and B, 8). Each of these last consists of a strong basal joint, which

* *Annals of Natural History*, 1854; Report on Edriophthalma, British Association, 1855.

supports two distinct appendages, the one consisting of five short articulations, the other of two long ones, terminating with four long finely-ciliated hairs.

The next pair of members differ little from the last, and represent the second pair of *gnathopoda* (Plate XL. figs. A and B, 9) in the adult. Like the preceding, each consists of a basal joint supporting two appendages, one of which is formed of three *short* articulations, the other of two *long* ones, furnished at the extremity with four long hairs delicately ciliated. At the base of these two last pairs of appendages, the germ of the future branchiæ may be distinguished. These two last pairs fulfil the office of natatory organs in this early stage of the animal.

Posterior to the last pair of members that I have described several sacs are visible (Plate XL. figs. A and B, 10). These evidently contain the germs of the five pairs of *pereiopoda*, or true perambulatory legs, the most anterior of which I think I have been enabled to perceive lying folded within the sac, as shown in Plate XL. fig. 10. Some of these small sac-buds probably are the germs of the future branchiæ; and it is not improbable that in this embryonic condition they fulfil the object of their design sufficiently well for so immature a creature.

We now come to the third division of the animal, the *pleon*, or that portion which in adult Crustacea supports the swimming legs. It consists at this stage of six segments; five upon one type, the last different. The first five are simple articulations, and carry no developed appendage, except two small tooth-like processes upon the second. But close observation will detect the germs of the future *pleopoda* (Plate XL. fig. 17) upon one or two, situated laterally and inferiorly. Each of them consists of but a simple bud, on the margin of which can be detected three or four clear bead-like spots, the rudiments of the undeveloped cilia.

There are no data by which to determine the homologue of the two denticular processes (Plates XL. and XLI. figs. B, C''', D'', 16) upon the second segment. They are directed forwards, and agree somewhat in position to the external organs of the adult male. They are constant upon all the specimens in this species, and in that of *Cancer Pagurus* also, the larva of which agrees so nearly with that of *Carcinus*, that it is doubtful if the closest observation could identify them apart. The *pleopoda* in an early stage are attached to all except the first and last of the segments of the *pleon*, but are present only in the adult female of the *Brachyura*.

If there be any truth in the hypothesis relative to the denticular processes upon the second segment, each animal must in its larval condition contain within itself the germs of both sexes. The one or the other becomes developed according to more or less favourable circumstances. If this be the case, it is not difficult to account for the occasional development of distinct sexes upon opposite sides of the same animal; or, as I have in my possession, a *Corystes cassivelaunus* bearing the aspect of the female, and yet possessing male organs.

The sixth or last appendage (Plate XL. figs. A and B, 21) to the larva homologizes with the last, or *telson* of the adult. It forms a prominently forked appendage, consisting of two

long slightly-curved styliform processes, armed upon the external margin with two or three teeth. Upon the inside, near the base of each, is a small lobe that supports three strong spinous denticulated hairs, and between the two lobes debouches the intestinal canal.

Having traced the structure of the individual parts of the larva as it exists immediately upon quitting the ovum, our next object will be to compare the same with others of later growth. Repeated moults, probably at intervals of seven or eight days, succeed each other, producing at each stage but little change to the eye but that of size. If we examine one probably a month old (Plate XLI. fig. C), it will be found to have acquired no distinct feature to mark it generally from the preceding. It has attained the length of two lines, that is, about as long again as the larva when it quits the ovum. The examination of individual parts will, however, exhibit some progress in the development of each member in relation to the whole.

The carapax differs not from that of the younger form, except that certain bead-like spots noticeable in the former have become developed into hairs in this. These exist mostly upon the long dorsal process and the posterior margin of the carapax. The eye has become more distinctly pedunculated, and appears capable of independent movement. The *anterior antenna* (Plate XLI. fig. C, 2) has the number of auditory cilia increased from two to eight or nine, and a small process (*d*) is discernible near the base of these cilia, which is evidently the secondary filament of the perfect organ. This goes on increasing with the succeeding moults. The stem of the organ exhibits a joint in the middle (Plate XLI. fig. D, 2), and the basal articulation considerably increases in diameter, so that before the animal throws off the larval condition, the anterior antenna has arrived at a point of development approximating to the character of the adult organ.

The second or posterior antenna (Plate XLI. fig. 3) likewise exhibits signs of progress. The squamiform (*g*) and spinous processes (*h*) are unchanged, but the small papilla at their base has increased, first to a length which scarcely equals that of the adjoining spine. In another moult it becomes longer (*f*, 3''). So it continues to increase, and with it distinct articulations, one probably being added at every moult.

The progress in the next succeeding pair (the mandibles, Plate XLI. D, fig. 4) is externally so little as to be scarcely appreciable. They appear more powerful in general structure, and the calcareous tendon and internal lever process can be detected by dissection.

The first pair of *maxillæ* (Plate XLI. D, fig. 5) have more cilia developed upon the margins of each plate; and a small lash (*z*) (the flabella of the adult organ) is likewise present; and it may be assumed, from the much greater relative size, that it fulfils a more efficient office in the larva than in the adult.

The second pair of *maxillæ* (Plate XLI. D, fig. 6) have likewise an increased number of ciliated hairs developed upon the margin of each plate; those upon the flabella have increased from four to a considerable number.

The next succeeding pair are still undiscoverable to the closest observation.

The two pairs of *gnathopoda* (Plate XLI. D, figs. 8 and 9) appear to have undergone

no change beyond an increase in their general size, and a little in the relative proportion of the appendages to the base on which they are supported, and the addition of a few hairs to the extremity of each.

We come now to that portion of the animal in which the greatest amount of progress is apparent. In the first stage we perceived a series of sac-like vesicles, the germs of the *pereiopoda*, which have since been gradually produced (Plate XLI. figs. C, 10 to 14), probably at the rate of a single articulation at every moult, since one or two are at first perceived, then more, and lastly the entire seven (figs. 10, 11' and 11"). At the base of the legs the future branchiæ may be detected in the form of simple sacs. The anterior pair exhibit at this early date the chelæ of the adult organ.

The *pleon* (Plate XLI. fig. C'') exhibits the seven segments proper to the adult. This increase appears to have taken place by the bisection of the posterior segment, with which it continues in close connexion. The three central segments have at the posterior lateral extremities of each a strong tooth-like process, and upon the inferior surface certain oar-like appendages—the undeveloped *pleopoda*. These rapidly increase and have their margins—those which are anterior being the earlier—furnished with small dots, the germs of the future cilia. Upon the second segment (figs. C''' and D'', 16), the two strong tooth-like organs projecting anteriorly and externally are still present.

The *telson* (C'' and D'', 21), or last segment, has lost some of the teeth with which the external margin was armed. Internally a few small hairs are added. The cleft between these appears less deep, and the styliform processes not quite so long.

Plate XLII. fig. E.—If we examine the growing animal after a few more moults, when it has increased to about three lines in length, we shall find its outline still holding a resemblance, though a less close one, to the previous appearance.

The form of the carapax scarcely differs except in the shorter relative length of the anterior and dorsal spines, and the whole animal appears stouter and more robust. The *gnathopoda* cease to be used as natatory organs; the *pereiopoda* are more fully developed, and assist in their proper capacity, and the *pleon* has lost its forked extremity.

Upon examining the several parts in detail, the organs are found generally to have progressed. The anterior antenna (fig. 2) differs scarcely from that in the adult. The posterior (fig. 3) has increased in length; the olfactory organ (*a*) is present in an immature form, and the appendages proper to the larval state are lost. The *mandible* (fig. 4) has assumed the form of the adult organ, and the appendage is present. The *maxillæ* (figs. 5 and 6) have progressed a little, but still retain some of their early conditions. The *maxilliped* (fig. 7), which is found wanting in the two preceding forms that have been examined, is now present, and differs in no very important feature from that of the adult. The *gnathopoda* (figs. 8 and 9) have considerably progressed, though they have not yet assumed (particularly the posterior) the form of the parent organ. The appendages on each have outgrown the basal articulation, which latter has sunk into an unimportant part. The first two joints have considerably increased, whereas the others, and their complementary appendage, appear not much changed.

The *pereiopoda* (fig. E, 10 to 14) have become organs sufficiently powerful to enable the animal to use them in walking. The anterior two or three pairs have a tooth-like spine attached to the anterior edge of the *coxa* and *basos*; and the branchiæ have assumed the compound character approaching that of the perfect organ.

The *pleopoda* (figs. 18, 19, 20) have all the external or secondary branches largely developed and furnished with plumose cilia, thus forming efficient natatory organs.

The *telson* (fig. 21) has no appendage. It is not forked as in the early period, but is imperfectly square and squamiform. On each side of the posterior margin the rudiment of the styliform process may still be observed in the form of a small denticle. The three central hairs still remain.

Soon other moults deprive the animal of the dorsal spine (Plate XLIII. F). But the loss of this peculiar feature in the external aspect of the animal, although the most apparent, is not, I think, the most important alteration at this period. The anterior margin of the carapax, including the rostrum, continues much depressed, but the lateral margin of the same anterior portion is much raised; there is also a considerable lobe (fig. F a, F'' a) developed on each side posterior to the eyes. The *upper antenna* (fig. 2) is more complete, and the internal structure of the acoustic organ (fig. 2') may be detected in the first articulation. The *second antenna* (fig. 3) has increased but little in length; and a few hairs, a pair of which are exceedingly long, are developed towards the tip. The *maxillæ* (figs. 5 and 6) are nearly of the same form and character as the preceding; so also are most of the succeeding members. Three small tubercles (*r, s, t*) are seen to be developed upon the oral margin of the posterior *gnathopoda* (fig. 9). The small protuberances, which were previously scarcely visible upon the *coxa* (*a*) and *basos* (*b*) of the anterior *pereiopoda* (figs. 10, 11, 12), have become developed into spines of considerable importance. The appendages (figs. 15 to 20) to the *pleon* have undergone no appreciable change. The *telson* (fig. 21) has lost the last rudiments of the styliform caudal processes; but the central hairs, still limited to three, remain as in the preceding.

Plate XLIV.—Successive moults rob the young animal soon of the frontal spine. Contemporary with its decreasing importance, the *pleon* becomes gradually folded nearer and nearer, until it is closely compressed against the inferior surface of the *pereiion*. Upon each side of the carapax posterior to the eyes four small denticles (*l, m, n, o*) are developed. These at first are scarcely visible in the contour of the animal, which has considerably increased in diameter at this point, where it is as wide as at the posterior extremity of the carapax.

The eyes (fig. G, 1) are still large and prominent. The organs (figs. 5, 6, 7, 8, 9) attendant upon the mouth in all essential points approximate nearer to those of the adult form; and where there is a distinction, it is in their resemblance to the younger stage. The *pereiopoda* are all strong and capable of supporting the animal in its perambulations. The spines upon the *basos* in the *pereiopoda* are gone, and the *pleopoda* have lost their natatory character and assumed an atrophied appearance (figs. 17, 18, 19, 20).

When the animal is a little larger, though still of the same form, the segments of the *pleon* in the male commence a fusion together. The intromittent organs are visible.

The animal (exclusive of the *pleon*) scarcely differs in appearance from the time when it was half a line long until it has reached to two and a half lines; even then the alteration in appearance consists chiefly in the increase of the animal on each side, and the comparative shortening of the interocular portion of the carapax. The eyes are still prominent, but the organs generally have assumed a closer resemblance to those of the adult form, from which they appear to differ but little. That which is most conspicuous in the animal, exists in the gradual extension of the post-orbital or hepatic regions.

Having pursued the course of development from the larva to the mature form of the *Brachyura* decapod, a moderate-sized specimen of which produces about two millions of ova, we perceive that the progress made is not by any sudden metamorphosis, but by a series of moultings similar to those which take place in the adult; and that with each successive moult there is a corresponding degree of progress in its development. But the amount of change at each moult is so little, that it gives to the animal but a very small degree of difference in its general appearance; and it is only by a comparison of the earliest form with the last, and that without any consideration of the intermediate stages in its growth, that the idea of a true metamorphosis in decapod Crustacea has existed.

There are six or seven well-marked stages or forms that the growing animal passes through in its progress to maturity, and each of these is linked to the preceding, as well as to that which follows, by a succession of changes that are but just appreciable.

The form of the *Zoëa* when it first quits the ovum is distinctly embryonic. The whole of the parts are confined within a case, which gives it an immature character. The great dorsal and frontal spines are confined and folded close to the animal, and all the cilia enclosed within the tunic or outer case extend but a very limited way beyond that of the true limbs, whereas the greater portion of each is drawn back within it. This is correct of every member, and the large caudal spines upon the *pleon*. Besides this, the whole animal exhibits the appearance of contraction within the tunic, the skin being seen to be corrugated, so that when the animal throws off the case it immediately increases considerably in size.

It undergoes the first moult within a very few hours after its exclusion from the egg, when it loses much of its embryonic appearance, and swims about with more apparent control over its movements, and evidently seeks its own food. It keeps near the surface of the water, and always directs its head towards the light.

The large dorsal and frontal spines are extended, and exhibit a marked peculiarity in this stage of the young creature. The latter represents the rostrum, and is scarcely more important than is found among certain *Macroura*; whereas the former is occupied by the heart, and evidently homologizes with the pointed tubercle, which is situated upon the cardiac region in *Stenorhynchus*, &c. These two appendages gradually disappear, or to speak more correctly, their importance is outgrown by the relative increase of the

other parts, since they can be perceived in their position less and less prominent until the young creature has obtained the more important features of the adult. Looking at the carapax dorsally, it gradually increases in breadth from the extreme point of the frontal spine to the eyes, when, leaving orbits for the eyes, it widens a little immediately behind them, and then again it increases in diameter unto the posterior margin.

The larva, like the adult, has the power of elevating the carapax. The current of water that laves the branchiæ flows in beneath the posterior dorsal and lateral edges, while a membrane unites the centre of the carapax with the pleon, and precludes the admission of water to the internal viscera.

The larval form continues with a slight tendency to an increase in the relative length and width of the whole until the hepatic regions (Plate XLIII. fig. *Fa*) become visible; and when these appear, the dorsal spine is lost, and the animal assumes the general aspect of a Decapod, approximating nearest in appearance to the form of the Spider-crabs among adults.

Soon after the hepatic lobes are visible, they become crowned first with one (Plate XLIV. G. *l*) anterior tooth, then two (*m*), three (*n*), and four (*o*). These ultimately increase in diameter and number, and become the latero-anterior denticulated margin of the adult *Carcinus*.

This margin on each side generally extends outwards and forwards, and the anterior tooth (*l*) becomes the outer limit of the orbit; while its under margin is formed by the carapax (fig. *G''*) being reflected inferiorly; its external limit, with the appendage which it supports—the second antenna (3),—being planted upon the inner side of the eye.

In the earliest form the eyes appear sessile. This, however, continues but a very little while. Before the animal has undergone a change in its general form, the eyes are elevated upon prominent footstalks. But even in its earliest stage this condition of the eyes is to our conception sessile, rather because the peduncle is limited, than because it is altogether absent. Thus in the genus *Cyprhiops*, DANA, of the southern seas, the eyes are hid entirely beneath the carapax, and in some of our (subterranean?) *Macroura* the peduncle is so short that the eye cannot readily be distinguished from the sessile form. This, which we find in the adult of different genera, is but a condition similar to that in the *Zoëa*. Thus in the *Macroura*, where the ophthalmic segment is absent, as I have observed in the young of *Orangon*, and has been represented in *Palæmon* by Captain DU CANE, the eyes are united at the base, as two organs springing from one origin; but in the *Brachyura*, where the ophthalmic segment is present,—though hid and very unimportant,—the eyes of the larva do not so closely approach each other; and, when seen dorsally (as in fig. *B''*, Plate XL.), exhibit evidences that they are actually pedunculated in this early stage*. With the development of these organs, the angle formed by the

* Since this paper has been laid before the Society, Mr. R. Q. COUCH has shown, in a paper read before the British Association at Dublin, and published in the 'Natural History Review' for October, 1857, that in *Palinurus*, in which the adult has the ophthalmic segment largely developed, the eyes in the larval condition are distinctly pedunculated.

reflexion of the carapax upon the inferior surface of the animal continues to increase, and, as previously shown, forms the orbit that protects the eye.

At first the *upper antenna* is embryonic (Plate XL. fig. 2) in its character, and bears a more imperfect appearance than is seen in any of the *adult* Crustacea, but approximates nearer to that of *Diastylis Rathkii* than to any of which we are aware. But, as we have before observed, there are conditions in the structure, even at this early period, which enable us not only to identify the organ with its homologue in the adult, but also to demonstrate the parts of it that are actually present.

In all adult Crustacea, as we have elsewhere shown*, the anterior antenna has upon each articulation of the filament two or more membranous hair-like appendages, which I have thought, from their being constant to the auditory antenna, and never found on any other part, to have an intimate connexion with the sense of hearing, and therefore call them *auditory cilia*.

When the animal throws off the earliest integumentary surface, there are but two of these *auditory cilia* visible; but their presence indicates not only that the organ is, as its position implies, the homologue of the anterior antenna, but that the germ of the future filament is present in a single articulation already developed. After several moults, two, three and more articulations appear successively, and a corresponding increase to the number of *auditory cilia*; and soon the germ of the secondary appendage is visible. We next perceive that the base of the organ has increased in diameter, and assumes a general form differing but little from that in the adult organ, and this while the animal is yet so young that it has lost nothing of its larval appearance.

In the mean time a corresponding change has taken place in the other organs. The second antenna is considerably produced in length, but as yet it has not assumed the form of the adult organ.

When first developed, as we have before seen, the second antenna consists of two branches springing from the same base. These branches we believe homologize with similar appendages to the adult organ, found mostly in the *Macroura* and *Anamoura* decapods. The true antenna springs from a small bud-like germ at their base (Plates XL. and XLVI. fig. B, 3).

The squamiform appendage in *Macroura* (the *Scaphocerite* of M. MILNE-EDWARDS'S later writings) universally springs from the *basos* articulation; and therefore it is the homotype of the *exognathe* or palp, which springs from the same articulation of each of the posterior organs of the mouth, and therefore holds the same relation (as we hope shortly to demonstrate) to the more important parts in the young stage of the so-called natatory feet of the larva.

The antenna originating from the almost invisible germ (*a*) progressively develops, but its secondary appendages remain with each successive moult unaltered. They decrease in relative importance, and are ultimately lost, and this considerably before the animal has assumed the adult form. But it is interesting to observe that these

* British Association Reports, 1855.

embryonic appendages are most commonly present in the adults of the lower forms of Crustacea.

Perceiving the squamiform articulation to be common to the larva of *Macroura* as well as the *Brachyura*, we are enabled to identify it as the homologue of the same appendage in the adult *Macroura*, and to state that the articulation from which it springs is the homologue of the *basos* articulation of the adult. Unlike as is the earliest condition of the second antenna to the mature organ, yet before the larva has lost the dorsal spine it has assumed much the appearance of the fully developed state, and exhibits upon the *coxa* the yet imperfect stage of the olfactory organ, which shortly afterwards is protected by a strong operculum, that permits the internal organ to be exposed, or shut out from external sensations. Early in its existence this antenna is attached at the base only, but in the adult form the lateral portion of the carapax has so increased upon its structure, that the filamentary termination only extends free (Plate XLV. fig. 3. XLVI. fig. 3, J); the peduncle, except the last articulation, without being actually fused, is closely incorporated with the surrounding structure, and forms the internal wall of the orbit, and becomes the partition between it and the foramen in which the anterior antenna is planted.

The mandible (Plate XLVI. fig. B, 4) likewise undergoes considerable changes between the early and late conditions. At first there appears no internal lever or calcareous tendon, but it consists of a strong denticulated curved scale articulating with the integument. It bears a near resemblance to its homologue in the Edriophthalmous Crustacea (fig. 4 Q). It is without the (mis-named) palp*, which appears soon after and is produced contemporary with the internal continuation or lever of the organ.

The *maxillæ* (Plate XLVI. figs. 5, 6) differ but in the relative dimensions of their respective parts from those of the adult; and the first, like the mandible, bears an extremely close resemblance to that of the Amphipoda (fig. 5 Q).

The next pair of organs present in the adult are wanting in the larva of the *Brachyura*. These are the posterior cephalic appendages, and are developed only contemporary with the *pereiopoda*. The absence of these last appendages appears peculiar to the *Brachyura*. My own observations on the *Macroura* support those made by Captain DU CANE, M. RATHKE, and M. JOLY, who describe three pairs of natatory feet as belonging to the larva of the *Macroura*.

The two pairs of appendages present in the young *Brachyura* homologize with the two pairs of *gnathopoda* in the adult (Plate XLVI. figs. 8, 9, A to J).

If the animal be examined after a few moultings, it will be found, as previously described, that the *pereiopoda*, which can be detected immediately after birth, are developed directly posterior to those existing in the larva. These have also been perceived by Captain DU CANE in *Palæmon* in the same relative position. Examination of these members individually enables the relative character of each to be detected. The

* The so-called palp is the homologue of the continuous joints of the member, and not a secondary appendage, and probably represents the fourth, fifth and sixth segments of the true leg.

anterior pair become the cheliform organs, and therefore homologize with the first pair of *pereiopoda*, the large-clawed legs in the *Brachyura*.

This observation is not supported by the researches of Captain DU CANE on *Palæmon*; but I have, in the dissection of the larva of an unknown *Macrowra*, removed the whole of the five pairs of *pereiopoda* from behind the larval appendages. Captain DU CANE'S observations appear to have been conducted by watching the animal in its habits and parts without dissection. I therefore feel more confidence in my own observations, since, by removing every member, I could examine each as to its individual form. These remarks are also supported by the opinion of RATHKE, who states that the larval natatory appendages homologize with the "three pairs of maxillipeds" of the adult; that is, the posterior pair of the cephalic region, and the two anterior pairs of the *pereiion*—"the *gnathopoda*." But, as I have previously stated, in the *Brachyura* the larva has but two pairs, and these homologize with the *gnathopoda* only.

Having established this position, we shall find that an examination of their development will confirm, by the forms that they assume, the correctness of these conclusions.

In the earliest form each of these organs consists of a *basal* articulation, that supports two separate appendages (Plate XLVI. figs. 8, 9, A). One, and this the more important (S), in this young condition exhibits alike in each pair but two articulations, the joint being only visible after being treated with liquor potassæ. The other appendage (T) differs in both pairs. It consists of five distinct articulations in the anterior (8), and but of three in the posterior (9). It is these two branches (T) that represent the true limbs of the adult. The others (S), without passing through any important change, become the secondary appendages in each.

There appears to be no very important alteration in the separate parts of the animal until the *pereiopoda* exhibit appearance of strength; but, in accordance with the changing condition in its habits from a swimming to a walking animal, the *gnathopoda* cease to be required as natatory organs: they consequently lose that power, proceed in the progress of their development, and assume that which enables them to fulfil the functions of external permanent organs attendant upon the mouth.

But the great distinction between the early and the late forms of the *Brachyura* is dependent upon the absence in the early stage of the *pereiopoda*,—the five posterior pairs of limbs belonging to the *pereiion*.

In the early larva, when it has just escaped from the egg, the rudiments, undistinguishable without care, alone are present, in the form of sac-like appendages. After a few moults they are visible to casual observation, and increase gradually in size, joint by joint, until they are of sufficient importance to assist as organs of locomotion. Gradually, as this state becomes more perfect, the *gnathopoda* lose their natatory character, and assimilate to those of the mature animal.

Posterior to these there are no appendages in the larva, but the germs of the *pleopoda* are capable of being detected shortly after birth. These soon increase to their greatest comparative extent. At the same time, the *pleon*, which at first had but six segments,

has completed its number by the addition of one immediately preceding the *telson*. In the larva of the *Brachyura* this new segment forms no very important part in the general economy, since the appendages, which exhibit a prominent feature in the later stages of the young condition, again assume an atrophied condition. But in the *Macroura* the appendages of the penultimate segment increase to a very considerable degree at a very early period, and together with the last segment form the fan-like caudal apparatus of the adult. According to the statement of RATHKE, in the larva of the *Anomoura* the posterior *pleopoda* are early developed to a considerable extent. Thus at this immature age this intermediate form exhibits conditions of a mixed character. It has the *Macroura* type posteriorly, while anteriorly it exhibits that of the *Brachyura*, in having only two pairs of natatory feet in the earliest state.

But perhaps of all the parts in the *Brachyura*, the posterior segment or *telson* is that which undergoes the greatest visible alteration of form, passing, as it does in the larva of *Carcinus*, from a large fork-like appendage to that which is exactly the reverse. The *telson* of the adult terminates posteriorly in a blunt point fringed with hairs. But even this extreme alteration is but the result of a succession of gradual changes. In the *Macroura* the change from first to last is not so great. It is little more than an elongation, without a corresponding increase in the width of the segment.

In contemplating the development of the decapod Crustacea, from the youngest and most anomalous form to that of the adult, we perceive that the greatest amount of change, both in appearance and the development of parts, takes place in the *Brachyura*; but that even here the change is no sudden transformation of one form into another, but a gradual and persistent growth, following each successive moult. Every part that is present in the larva, though not permanent in itself, is to be found in a permanent condition in one or other form of adult Crustacea. And moreover, those appendages which play the most important parts in the larva, fulfil only secondary conditions in relation to the adult. Thus the large natatory limbs in the larva become the palps of the adult *gnathopoda*, and the appendages of the second antenna either represent unimportant parts of the same organ, or are altogether wanting. Again, we perceive that certain parts which continue present with but a small amount of alteration, such as the mandibles and the maxillæ, bear a close resemblance of form to the same organs in adult Crustacea of an order lower than the parent of these. Again, where development of new parts takes place, it follows a law that is in accordance with the absence or presence of the same parts in Crustacea in the descending grade. Thus we find that the posterior segments are those which are not present in the anterior and second division of the animal; but in the *pleon*, instead of being the last, it is the penultimate that is wanting.

Among the *Amphipoda* there are certain forms more or less perfect in their complete character. In the descending scale we perceive that the penultimate segment of the *pleon*, with its appendages, first becomes rudimentary, as in *Cyrtophium*, and ultimately disappears, as in *Dulichia*, before any other segments of the *pleon* are affected by the depressing change.

Perceiving that in its passage to maturity the larva of *Carcinus* passes through forms that are known to be adult, it is legitimate to infer that those forms hold a lower grade in the rank of perfect animals than the adult *Carcinus*. When it first exhibits conditions that approximate to the decapod character, it bears a very close resemblance to the triangular *Brachyura*. This gradually disappears with the development of the hepatic regions, and the constantly increasing resemblance to the form of the adult.

The *Leptopodiadæ* have generally been ranked by carcinologists as the highest of the crustacean type; but the similarity of their appearance to an immature form of the young *Carcinus*, is a circumstance that must induce the philosophical naturalist to reconsider the subject. It is not without a knowledge of the facts upon which zoologists have adopted the arrangement, that the above remark is made.

Carcinologists generally admit that consolidation of the nervous system is a marked elevation in the character of the animal, and Professor DANA has enunciated the doctrine, that "a centralization of the nervous ganglia is true cephalization."

It is true that in the Spider-crabs there exists no hollow space in the centre of the consolidated ganglia; but those which are thus consolidated homologize with the separate ganglia that supply the limbs of the animal with nerves, not with those ganglia that supply the organs that are endowed with the power of sensation.

This idea receives support from the known characters of the respective animals. The *Portunidæ*, of which the *Carcinus* is placed as the highest form, are active and vivacious creatures, whereas the *Leptopodiadæ* are inanimate and sluggish, fulfilling in their habits the existence of the fakirs of eastern tradition; they continue so long without movement, that weeds take root upon their surface, the growth of which prevents them from being distinguished from the surrounding objects.

Again, the general littoral character of the *Portunidæ*, and of *Carcinus* in particular—which differs not widely in form from the terrestrial *Gegarcinus*—together with the fact that all the *Leptopodiadæ* are deep-sea genera, is in accordance with the doctrine laid down by Professor AGASSIZ, that all land and freshwater animals assume a higher and more perfect form than their allied types of the ocean.

DESCRIPTION OF THE PLATES.

- Fig. 1. The eye.
 Fig. 2. Anterior antenna. 2'. Internal structure. d. Secondary appendage.
 Fig. 3. Posterior antenna:—a. Permanent antenna. g. Squamiform process. h. Styli-
 form process.
 Fig. 4. Mandibles; Q. of Amphipoda. (*Talitrus*.)
 Fig. 5. Anterior maxilla; Q. of Amphipoda.
 Fig. 6. Posterior maxilla.

Fig. 7. Maxilliped.

Fig. 8. Anterior *gnathopoda*.

Fig. 9. Posterior *gnathopoda*. 9'. Point of ditto, to show the position of the cilia before the first moult.

Fig. 10 to 14. Pereiopoda:—*a*, Coxa; *b*, Basos; *c*, Ischium; *d*, Meros; *e*, Carpus; *f*, Propodos; *g*, Dactylus.

Fig. 15 to 20. Pleopoda.

Fig. 21. Telson. 21'. Exhibits the terminal process as folded within the outer case before the first moult. 21''. Ditto, undergoing change. 21'''. Ditto, undergone change.

S. Secondary appendage.

T. Principal appendage.

x, *y*. Branchia.

z. Flabella.

The numbers throughout refer to the same parts and represent the homological relation of each to the segment from which it is derived.

The small letters have also a similar value in relation to each individual part.

The Roman capital letters A, B, . . . K, signify the stage.

PLATE XL.

Illustrations of the Development of Carcinus Mænas.

Fig. A. Larva immediately as it quits the ovum.

Fig. B. Larva after first moult.

Fig. B'. Cephalic region seen from front.

Fig. B''. Cephalic region seen from above.

PLATE XLI.

Fig. C. Larva after two or three moults.

Fig. D. Appendages of larva a little older.

PLATE XLII.

Fig. E. Larva after several moults, seen in profile.

Fig. E'. Ditto ditto, seen dorsally.

Fig. E''. Carapax seen from beneath. It has one eye, one anterior and one posterior antenna *in situ*.

PLATE XLIII.

- Fig. F. Larva somewhat older than the preceding.
Fig. F'. Ditto ditto, viewed dorsally.
Fig. F''. Carapax with the eyes, one anterior and posterior antenna *in situ*, seen from beneath.

PLATE XLIV.

- Fig. G. Larva as it approaches the character of the *Brachyura*.
Fig. G'. Carapax viewed from beneath.
Fig. G''. Carapax seen in profile.
Fig. H. Young *Carcinus*, approximating nearer to the adult form.
Fig. H'. Carapax seen from beneath: left anterior antenna removed.

PLATE XLV.

- Fig. J. Adult *Carcinus*, viewed dorsally.
Fig. J'. Adult *Carcinus*, viewed ventrally.

PLATE XLVI.

- Fig. K. Diagram illustrating the forms of the carapax in its passage from the larva to the adult *Carcinus*. Fig. A *et seq.* The progressive development of parts.

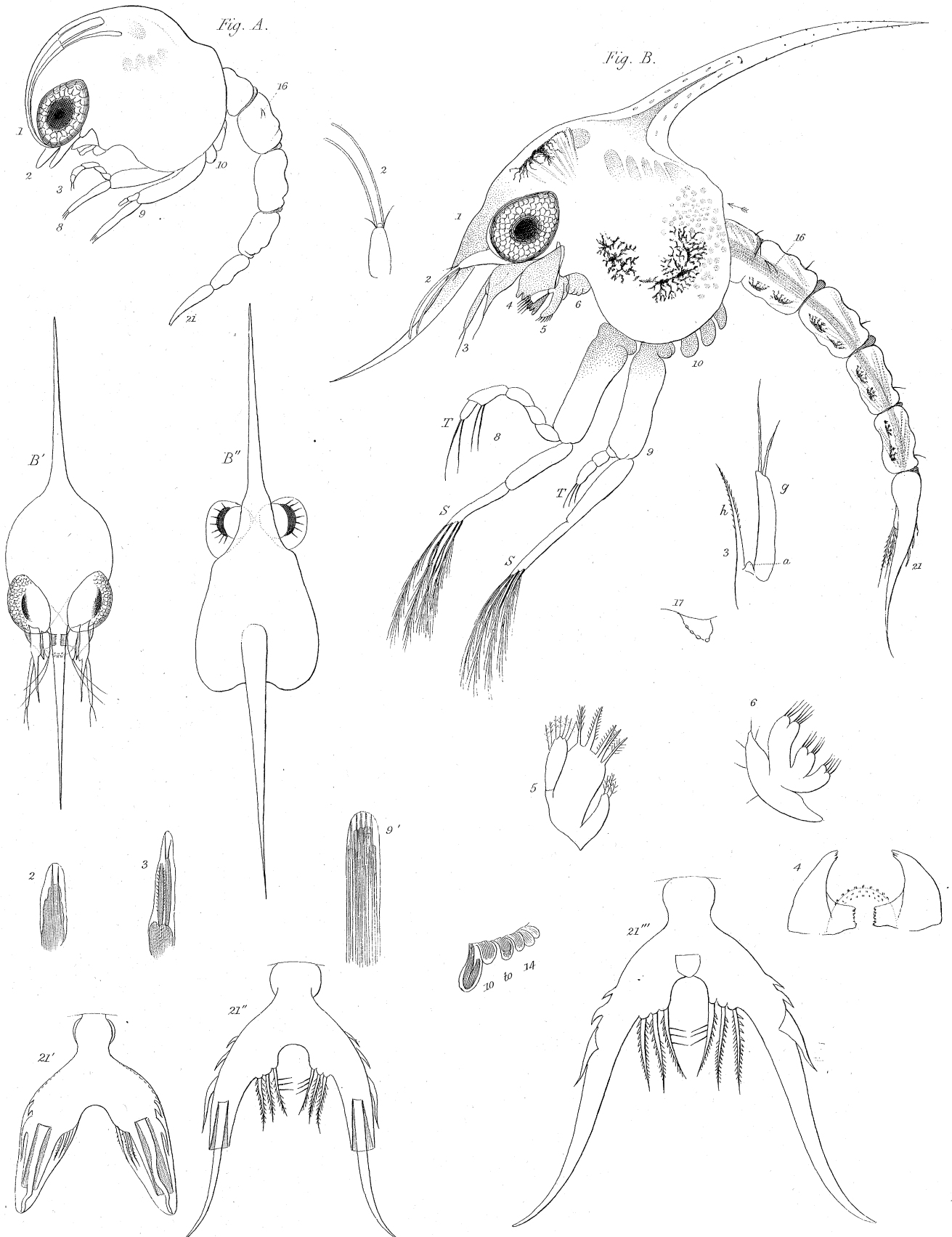


Fig. C.

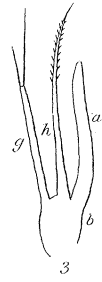
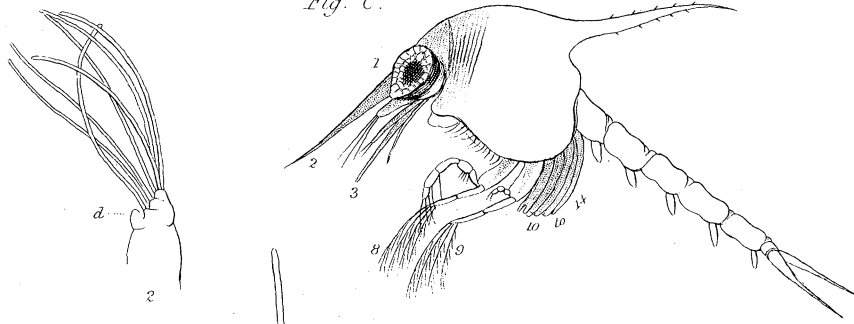


Fig. D.

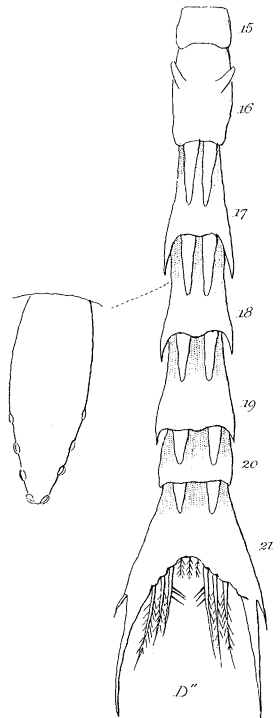
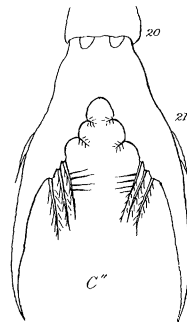
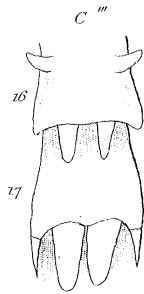
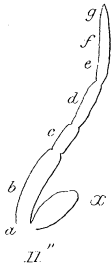
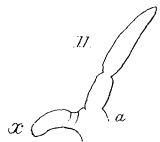
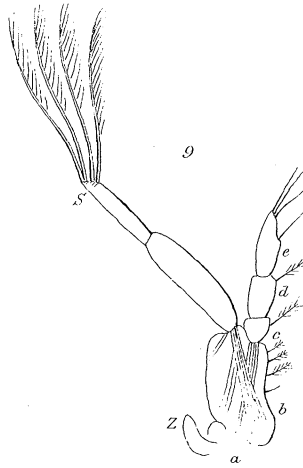
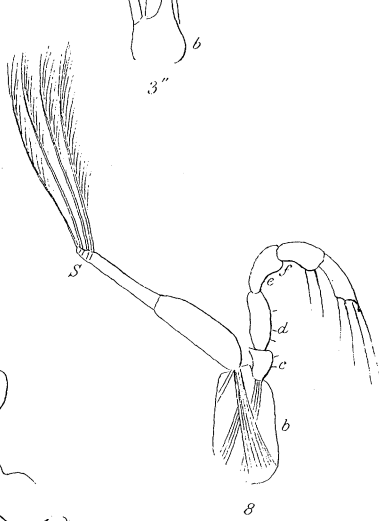
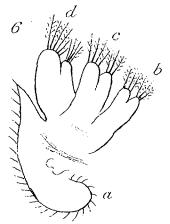
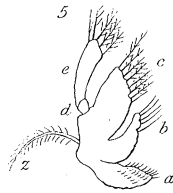
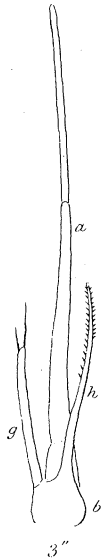
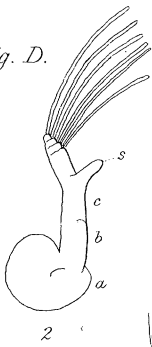
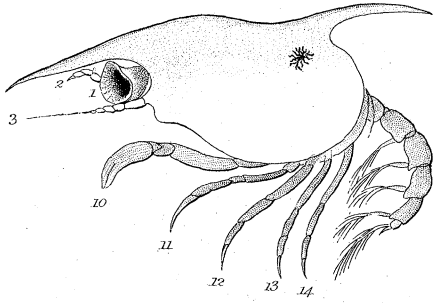
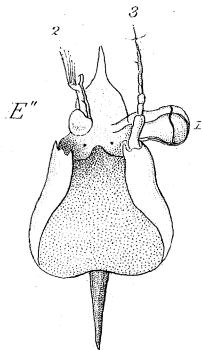
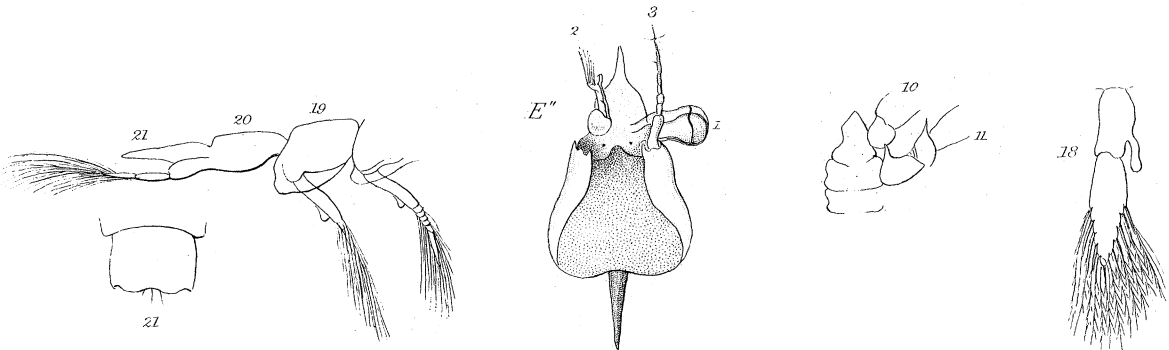
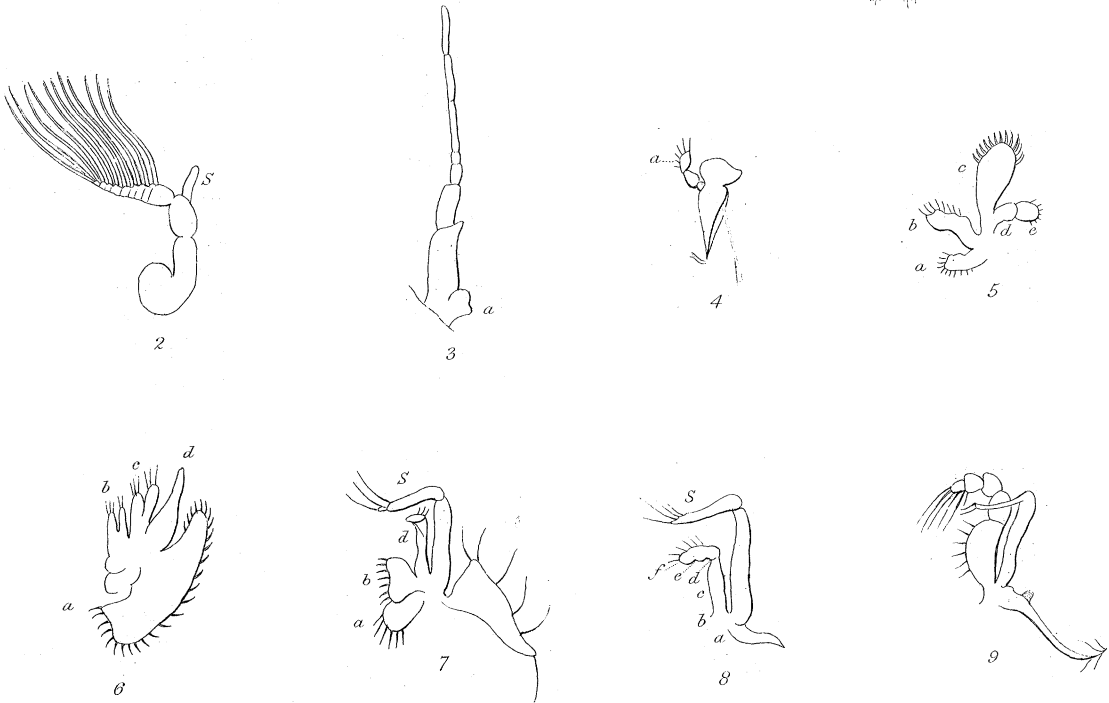
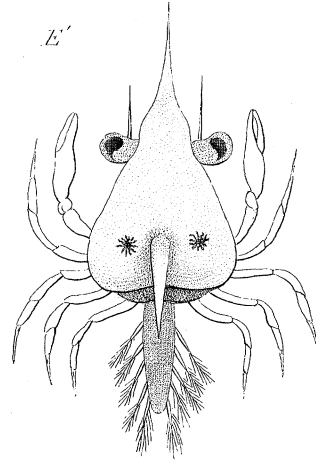


Fig. E.



E'



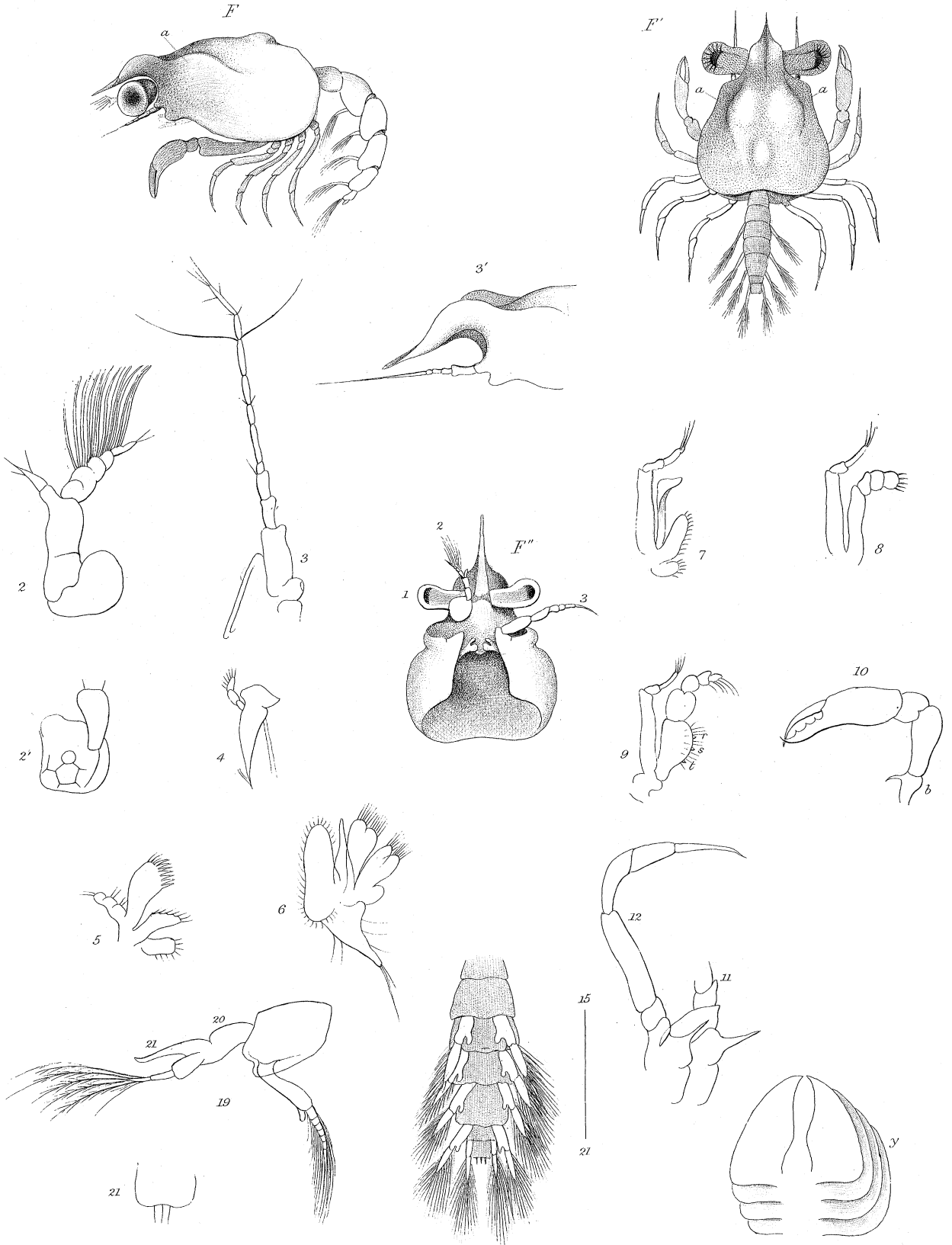


Fig. G.

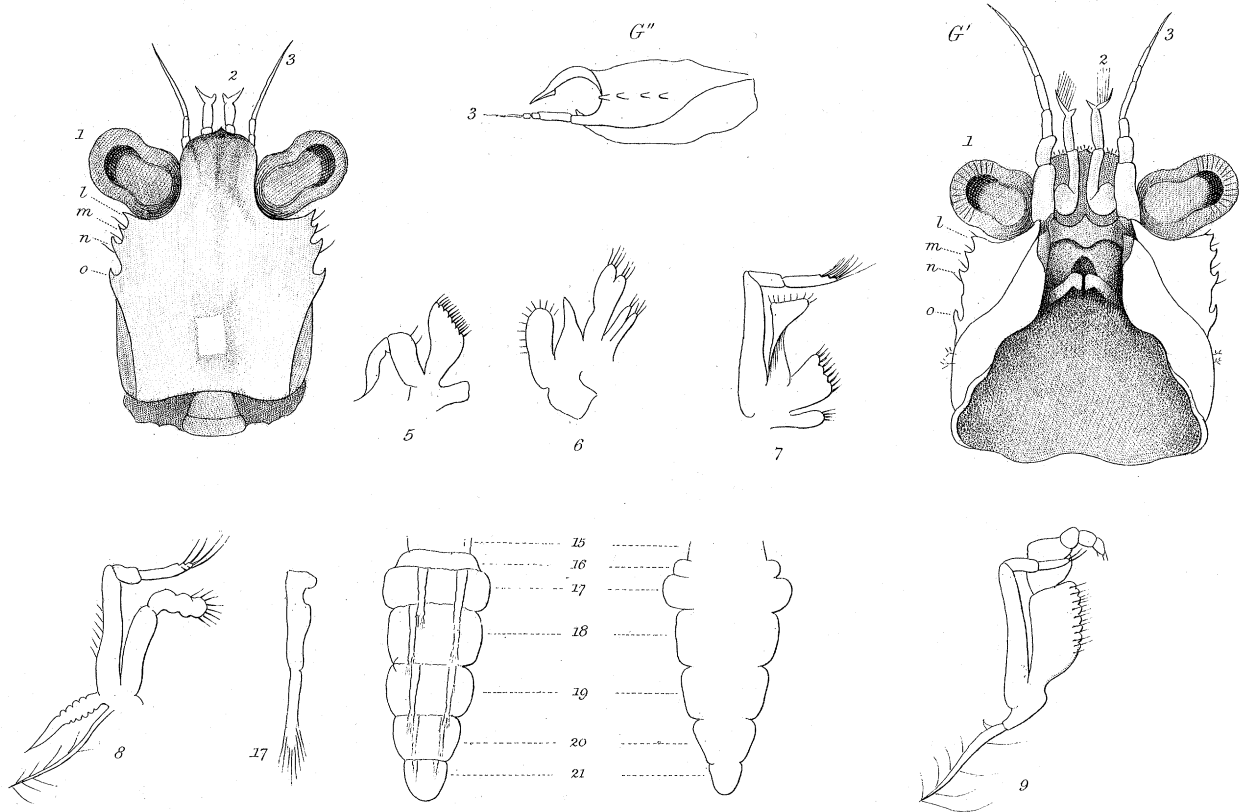


Fig. H.

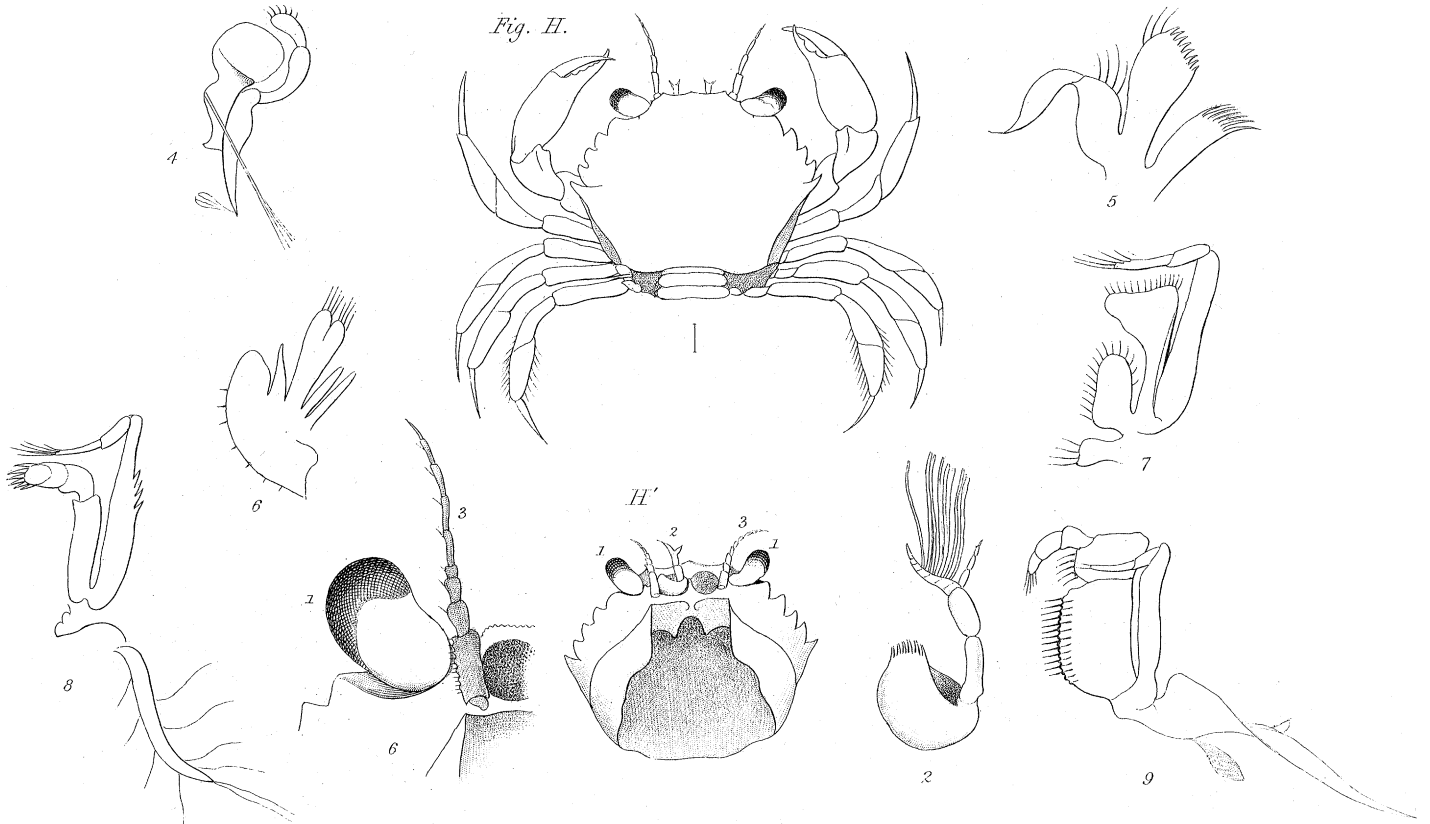
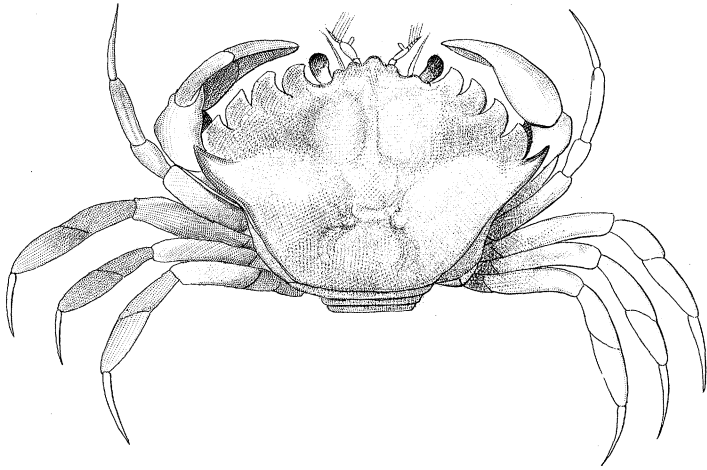


Fig. J.



J'

