

Expedition taken in the Atlantic near Madeira, off Cape Palmas and from the Indian Ocean between the Seychelles and Dar es Salam on the African coast, depths up to 4000 m. The description was only preliminary and without figures. GURNEY (1936) later gave a more detailed description with figures and a reconstruction. This reconstruction he later abandoned (1942), now considering the carapace flattened and not inflated as he did in 1936. He still called it *Amphionides valdiviae* and considered it a different genus and species, although closely related to *Amphion* as described in his 1936 paper. Later, GURNEY (1942) felt convinced that *Amphionides* was the adult of *Amphion*. But he could not prove it, although to judge from both ZIMMER's and GURNEY's descriptions, both have seen the same transitional stages as here described as Postlarva I and II. However, they interpreted both these stages as females of *Amphionides*, although a closer examination, as I hope to have given here, clearly shows that they are only transitional developmental stages between the surface larva *Amphion* and its abyssal-living adult, *Amphionides*.

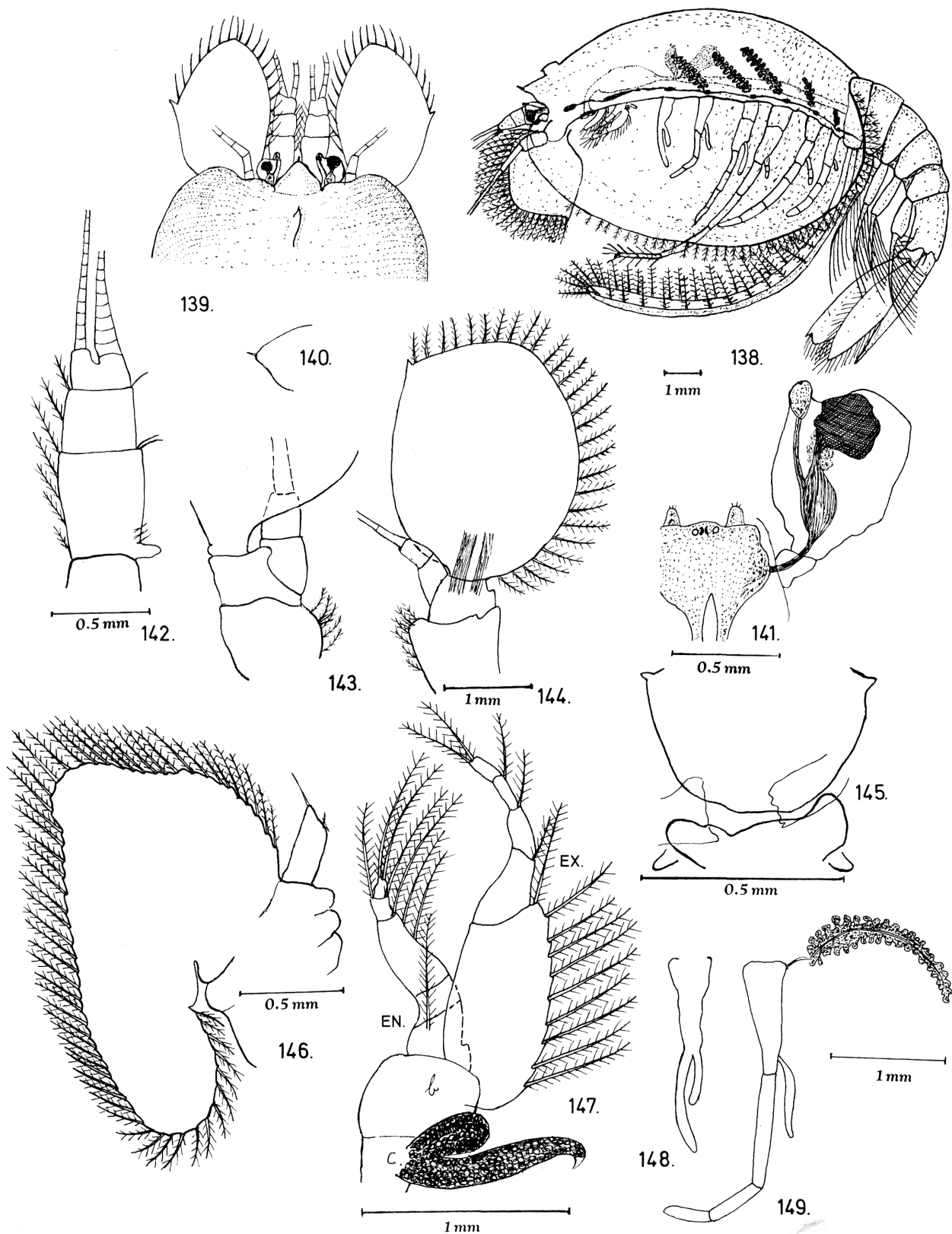
The reconstruction of the adult *Amphion* is rather difficult because, as GURNEY (1936) so rightly writes, "the thoracic region of these specimens is like a mass of torn and sodden tissue paper", or it reminds one of "*Beroe*" found in lumps in a plankton haul, only without the ciliated ribs, a picture all marine zoologists have seen. As I have had several specimens from the "Dana" expedition and three from "Discovery", the latter kindly lent to me by the British Museum, I have tried to make a new reconstruction based on the specimens, and I think GURNEY's first idea of an inflated carapace was right. I have constructed it even a little more inflated, a result I gained by placing the torn pieces together from some of the best-preserved and least-damaged specimens (Fig. 138). Another difference from previous descriptions is that according to its structure, the first pleopod in some of my specimens (where it is best preserved) is a definite feeding organ, and in none a secondary male sexual organ — this shall be discussed later. This new examination, based in part on new material, has provided more morphological details of the species, and I therefore feel justified in redescribing *Amphionides* (possibly the adult of *Amphion reynaudi*), although no proofs of adulthood such as sexual characters have yet been observed in any specimens. Where such characters have been described in previous literature they are to be regarded as misinterpretations.

Development.

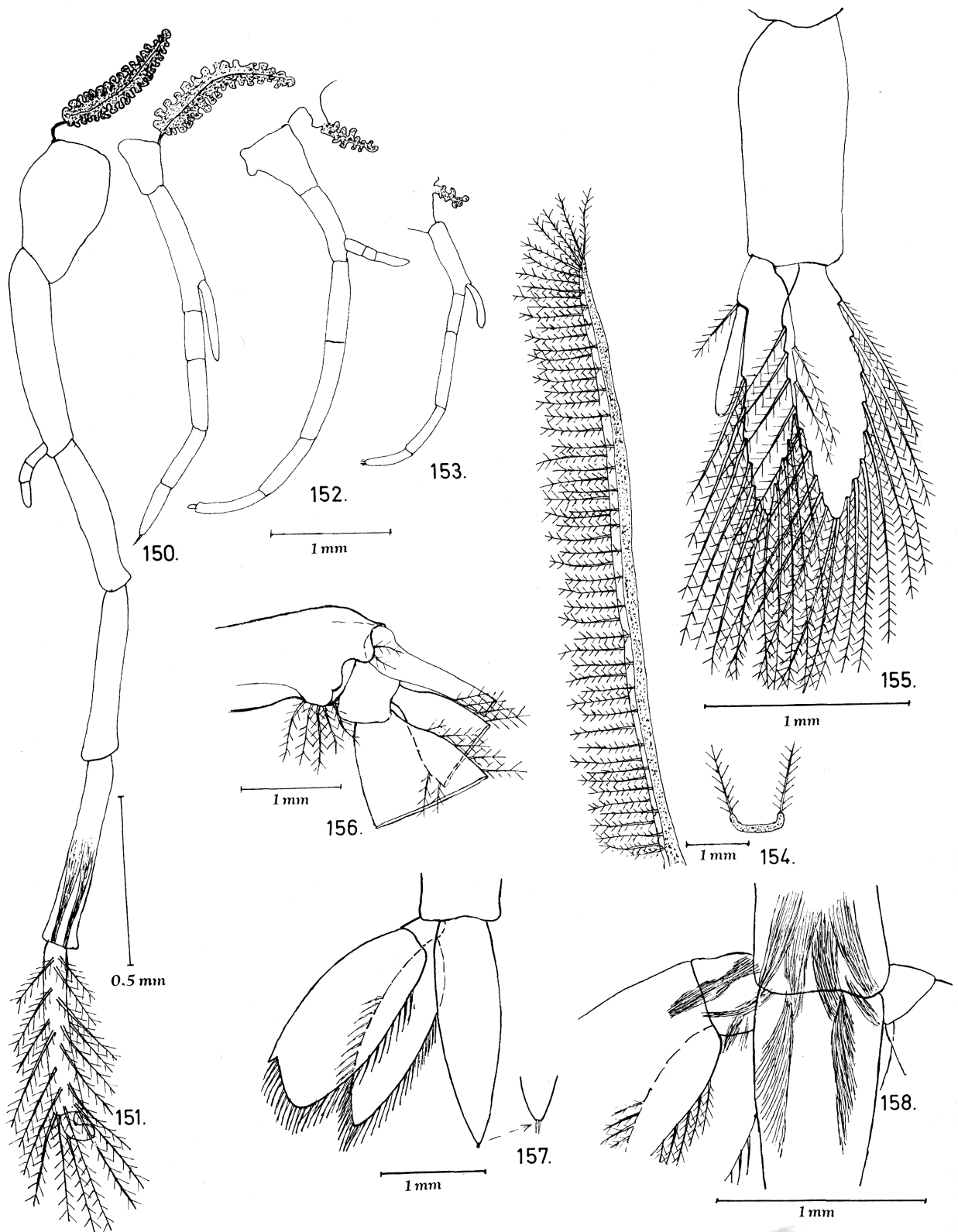
The carapace has finally grown to its full bell-shaped form. The orbital and antennal lobes of the carapace have enlarged. The marginal setae on the carapace have developed. The cuticle has become thinner on the carapace as well as on the abdomen. The muscles of the abdomen have strengthened and the lateral process on the first abdominal segment seems to have disappeared. The luminescent organ in the eye is fully developed and functional. Lenses have developed for the nauplius eye, but are still placed at a small distance from the eye cup. In the alimentary canal the cardia have enlarged and the pylorus and hepatopancreas have decreased. The rectal part seems to begin already midway in the thorax.

The basal joint of the first antenna has developed a medial process just below the point where the statocyst should invaginate. The antennal scale has widened and become more squarish. The mandibles and first maxillae are further reduced. On the second maxilla the endopod and the endites are also further reduced but the exopod has enlarged. In the first maxillipede both endopod and exopod consist now of five joints. The second and third maxillipedes, together with all the pereopods, except the second, have been strongly reduced; they seem in general to be non-functional. The second pereopod is further enlarged and the fourth joint of the endopod has developed many stiff plumose setae on its surface, similar to a lamp brush, and the fifth joint has become shaped like a blunt hook. The exopod is three-jointed and further reduced. The gills are unchanged from the previous stage.

The first pleopod (Fig. 154) has reached its peculiar shape, like a narrow canoe with a line of stiff plumose setae along the two gunwales and in the distal bow. The following five pairs of pleopods are normally shaped; they have enlarged, their swimming setae on the exopod and endopod having doubled in length. The appendix interna is well set off from the endopod in a movable joint. The telson plate has narrowed and is furnished with a tiny pair of hairs at the tip. The musculature from the body into the second antenna, the uropod and the telson plate has increased in size and seems to have developed additional fibres.



Figs. 138–149. *Amphion reynaudi*, adult. Fig. 138, in total from lateral. — Fig. 139, anterior part from dorsal. — Fig. 140, rostral plate and rostrum from lateral. — Fig. 141, brain with nauplius eye embedded in its tissue and dorsal frontal lobes sticking forward, lateral eye with luminescence organ at its dorso-medial side with a strong nerve from the plexus in the eyeball. — Fig. 142, right first antenna from dorsal. — Fig. 143, basal part of second antenna from dorsal. — Fig. 144, second antenna from ventral. — Fig. 145, mouth region with labrum, mandibles and labium, and vestigial first maxilla in the corners below. — Fig. 146, second maxilla. — Fig. 147, first maxillipede. — Fig. 148, second maxillipede. — Fig. 149, third maxillipede with its pleurobranchia.



Figs. 150–158. *Amphion reynaudi*, adult. Figs. 150–153, first to fourth pereopod with their pleurobranchia. — Fig. 154, first pleopod. — Fig. 155, second pleopod. — Fig. 156, last abdominal segment with part of telson and left uropod. — Fig. 157, telson plate and left uropod. — Fig. 158, parts of sixth abdominal segment, telson plate and uropods, all from dorsal to illustrate the strong musculature.

Thorax.

After a reconstruction of the thorax with its soft tissue-paper-like carapace (Fig. 138) the latter seems to be globular or semiglobular to elliptical. Specimens with an intact carapace margin clearly show that it cannot be flattened as in the older stages of *Amphion*, but that it is clearly inflated, with the nerve cord running as a string down a medial line from the brain into the abdomen. Dorsally on the brain is placed a double nauplius eye (Fig. 141), not unpaired as described by ZIMMER, with two distinct lenses slightly lateral to the retina cup and not yet enclosed in it. This is a further development from the surface form where lenses never were developed. The brain is divided into a medial part in which the nauplius eye is placed and two lateral lobes which posteriorly extend into the nerve cord; anteriorly there are two relatively large lobes, the dorsal frontal organs, while the ventral ones are smaller and placed more closely together. A strong nerve runs from the brain into the eye where it, after passing a short eye stalk, widens into an open cone or spindle-shaped ganglion spreading its neurons out into the retina cells.

From the dorsomedial side of the spindle-shaped ganglion in the eye a nerve string goes to a bulb placed dorsomedially at the frontal corner of the eye. This is the luminescence organ, which already had started to develop in the previous stage but first is functioning in this adult stage (see Fig. 141). This luminescent organ has a small anterior opening in the bulb, pointing directly forward, and must be able to project a narrow ray of light to a short distance in front of the eye. As the eye is movable, the ray can be directed to the sides as well as at least in an angle of maximum 45° upwards and downwards, limited to the eye's own mobility. The eye itself is much swollen, which may have been caused by the pressure change from depth to surface. A glandular mass seems to be placed between the retina cells and the spindle-shaped ganglion of the eye, as shown on the figure.

Dorsal to the nerve cord is the alimentary canal, with a short oesophagus running between the nerve commissures into a thin-walled swelling, the stomach. Of the latter no closer details could be ascertained, except that the cardia is shaped like an elongated cylinder and the pylorus is very diminutive. After the stomach follows a short, narrow enteron, from which two pairs of small grape-like glands, the hepatopancreas, extend. In the surface form of *Amphion*, as shown in GURNEY's illustration (1936, Fig. 12b), the hepatopancreas has two lobes, one anterior, much branched, and one posteriorly directed, less branched and passing through most of the thorax. Already in the previous stage the anterior lobe has started to become smaller and the posterior lobe to shorten in length. Now they are small sausage-shaped organs with a glandular capacity which, judged by their volume, is much less than in the surface form, a fact also agreeing with *Amphion*'s new habitat and mode of life, in which the intake of food is probably diminutive when compared with the feeding possibilities for the surface form. After the enteron follows an intestine which again widens a little and possibly only functions as a rectum. It has rather thick and muscular walls, showing that it must come from the proctodeum. It continues as a true rectum through the abdomen.

The carapace extends laterally and ventrally as two large, semiglobular lobes fringed by hairs along the posterior two thirds or more of the margin. In some specimens these plumose setae reach forward in line with the partly backwards-bent antennal plates (Fig. 138). In front, the carapace continues as a fleshy rostral plate (Figs. 138, 139, 140) without any movable link to the carapace. From the anterior tip of the rostral plate the, for *Amphion* characteristic, rostrum projects as a small stick. Behind the rostral plate is the post-rostral spine or anterior dorsal organ, with a bulb and a single forward-pointing spine. Lateral to the rostral plate the orbital and the antennal lobes have enlarged, and especially the antennal lobes dominate so much that the orbital lobes can look like a secondary lobe on the antennal lobe (Figs. 138, 139).

Abdomen.

The abdomen is strongly developed and more characteristic of a postlarval than a larval stage. Its musculature shows a high development and each segment continues ventrally with a muscular lobe to each limb from which the pleopods extend. The whole abdomen is smooth, without spines, and the cuticle is thin, causing the pleura on the preserved material to be a little swollen. On the last segment (Fig. 156) the cuticle runs out into a small lobe fringed with two or three plumose setae and covering the base of the telson plate on

each side. More ventrally and covering the base of the uropods is another bipartite lobe, of which the ventral part is fringed with a line of soft plumose hairs or setae. The lateral process may be present in the adult, but could not be clearly distinguished on the present material.

Telson.

The telson plate (Figs. 135, 136) is a long elliptical, posteriorly pointed, plate with a smooth surface. It is of interest to note that it is furnished with unusually strong muscles which must make it possible for the shrimp to move it together with the uropods with a considerable force. It is posteriorly tipped with a pair of minute spines or hairy setae.

Appendages.

The first antenna (Fig. 142) is placed on a small forward-pointing lobe of the thorax and consists of a three-jointed, very stout peduncle, without otocyst but with the medial otocyst process on the basal joint well developed. The joints decrease in size distally, the basal joint being as long as or even longer than the two others together. On the medial border of the peduncle is a line of plumose setae. Opposite on the lateral side small setae are placed distally on the first and second joints. The last joint is tipped with two flagella which always were broken near the base. The lateral flagellum is much broader at the base than the medial one, which is thin as a thread from its very beginning.

The second antenna (Figs. 143, 144) has a short coxa and basale, the former with a line of small, plumose setae on the lateral margin. The exopodial antennal scale is a large, squarish plate with a short apical spine and shorter, plumose setae along the distomedial margin. The endopod consists of two basal joints of about equal length and a thin flagellum which on all the specimens was broken near the base.

The mouth opening (Fig. 145) is covered by the labrum, which has widened and reaches towards the labium of which the two lateral lobes have diminished. GURNEY wrote (1936, p. 398) "Mandible not seen. Maxillule vestigial, apparently represented by a pair of small papillae, without setae, on either side of upper lip." Unfortunately no further description is given of the labrum and on his figure 13 the lobe drawn in front of the first maxillipede must represent the scaphognath of the second maxilla. Below the opening between the labrum and labium the mandibles are placed. Behind the labium are two small lobes representing the vestiges of the first maxillae. I have, like the previous investigators, also had considerable difficulties in analyzing these mouth parts, because the material at my disposal is very defective. I have, as shown in Fig. 145, tried to give the relationships and placement of these mouth parts.

The second maxilla (Fig. 146) has a short, squarish peduncle in which both coxa and basale can be distinguished, but without a clear suture between them. The masticatory endites are further reduced and very diminutive. The endopod is short and vestigial. It has become thinner and more delicate than in the previous stage, and is tipped with two small setae. The exopod or scaphognathal lobe is large for the size of the limb, with the typical anterior and posterior lobes and with the anterior part extraordinarily wide, giving the scaphognath a rather characteristic shape.

Close against the second maxilla is the first maxillipede (Fig. 147). It consists of a short stalk-like coxa with a two-lobed exite functioning as a double mastigobranchia; its anterior lobe, which just had started to develop in the previous stage, has here developed to half the length of the posterior lobe. The basale is much larger than coxa, but without endites. The exopod is five-jointed. The large basal joint has a lateral crista with a comb of long, stiff, plumose setae along its lateral margin. The four following joints are much smaller and decrease in size and width distally. Each of the first four joints has a single plumose distolateral seta, and the fifth is tipped with two setae. The endopod is shorter, about two thirds the length of the exopod, and is also five-jointed. Up to this stage it has been only three-jointed, but through enlargement of the whole branch, the first and third joints of the previous stage have both become divided into two joints, and the second has grown in length. The endopod is furnished with a sweeping comb of plumose setae, which are even longer than the ones on the exopod and mostly placed on the distal half. The maxilla and the first maxillipede are now clearly functioning as feeding organs, and they have therefore undergone this further development.

The following appendages are not directly concentrated near the mouth, although the two following limbs may be named maxillipedes as in the rest of the decapods; however, they have no function of this kind either in *Amphion* in its surface form or in the abyssal adult. They are placed farther back, together with the thoracopods, and developed like these. The second maxillipede (Fig. 148) is only vestigial, bifurcate but unjointed, with the endopod twice the length of the exopod and without gills. The third maxillipede (Fig. 149) is a little larger and the endopod is three-jointed, but the whole limb is vestigial without any function, except for the large pleurobranchia at its base. The exopod is represented by a small, thread-like distolateral lobe from the protopod.

The first pereopod (Fig. 150) is similar to the third maxillipede, only a little larger and with a protopod divided into coxa and basale, the latter three times the length of the former. The exopod is unjointed and much like the one of the third maxillipede. The endopod is five-jointed, the tiny claw at the tip considered as the fifth joint. This seems an interesting point. Through all the larval stages in the surface-living *Amphion*, where the endopod was functional and an important prey-catching organ, it never consists of more than four joints, but now in its vestigial and nonfunctional form in the adult most endopods have become five-jointed, which is the normal among Malacostraca. The first pereopod seems to be without function. At its basis is a large, well-developed phyllobranchia. In the second pereopod we have again a functional limb (Fig. 151). The protopod consists of two joints, the coxa is the shorter and stouter and is only half as long as the basale. From the distal margin of the basale extends a small three-jointed, thread-like exopod. The endopod is five-jointed and two and a half times the length of the protopod. The first four joints are long and slender, the last joint is shaped as a peculiar bulbous and fleshy hook.

Strong muscles extend from the third into the fourth joint, making it possible for the fourth and fifth joints to move freely in all directions. The fourth joint is furnished with long, stiff, plumose setae along its whole surface, so that it looks like a lampbrush. Together with the first pleopod, its function must be to filter plankton brought inside the bell of the carapace and push it into the mouth, a process which shall be discussed after the description of the first pleopod. At the base of the limb is a well-developed pleurobranchia.

The third and fourth pereopods are again vestigial. The third (Fig. 152) is of about the same size and shape as the first pereopod. The protopod is divided into coxa and basale, here of about equal lengths. The small filamentous exopod is three-jointed. The endopod is five-jointed, consisting of four nearly equal joints and a fifth joint which only is a small bud or wart on the tip of the fourth joint. A rather small phyllobranchia is connected with the limb and appears to be placed on the tip of a small lobe from the body wall; possibly this lobe may be a bare proximal part of the gill. The fourth pereopod is still smaller (Fig. 153) and the protopod and the filamentous exopod are again unjointed. The endopod is much like the one in the third pereopod only shorter, more delicate and four-jointed, but it has a tuft of tiny hairs on the tip of the last joint. A vestigial pleurobranchia is attached to the limb. As in the preceding stage no fifth pereopod was developed.

The first pleopod (Fig. 154) is again extraordinarily well developed. The transformation of the first pleopod, which started in the previous stage, has been finished in the adult. A pair of immovable lobes extends from each segment. From the tip of these lobes the pleopod arises, making the lobes look like basal joints. This is especially characteristic for the first pleopod. These lobes, as mentioned on p. 52, seem to be an artificial product caused by shrinking of the surrounding parts. The cuticle is thin and does not give much resistance against shrinking. The wrinkles of the cuticle and its lack of fitting to the body show also that such a shrinkage has taken place. The body parts filled with massive muscles will shrink less than the more soft parts, what also explains why the first pereopod with its strongest muscles is placed on a larger lobe than the following pleopods. In the material brought to the surface, these have become extruding lobes. The first pleopod is a long flexible but unjointed and unbranched organ. The jointing from the previous stage has been entirely lost. In cross-section this pleopod looks like a barge (see Fig. 154) with a row of long, stiff, plumose setae on the margin, and at the tip it is closed like a boat stern. This organ has about the length of the carapace and can reach forward beyond the mouth appendages. Unfortunately, due to its unbranched nature, it has previously been associated with the male copulatory organs, with which I cannot see it has anything to do. It must

be a feeding organ. The adult has no proper biting or tearing organs. It lives pelagically in a depth of more than 2000 m in the open ocean, where the bottom is still much farther down, and must therefore be a plankton feeder. Its carapace is shaped like a bell and circular muscle fibres can be seen along its margin. Thus the adult most likely filters or catches small plankton organisms by means of its bell-shaped carapace. When the prey is inside the bell the carapace is closed, partly by its sides with their lines of stiff hairs being bent ventrally towards one another, and partly by the first pleopods closing the opening between the two halves of the carapace. With undulating movements and by help of the long setae the first pleopods can then push the prey organisms up towards the mouth. Simultaneously, the "lamp-brush" organ of the long second pereopod can move up and down like a piston in the free space between the carapace halves, and finally its hook-shaped last joint can push the food in between labrum and labium. Most likely the first pleopod can also be used to shovel planktonic organisms from the free water masses into the open bell formed by the carapace. When sufficient plankton organisms have been brought inside the bell, it closes and the food is filtered from the water and pushed into the mouth mainly by the second pereopod. Although, this may sound rather fantastic, one has only to remember the feeding process of many shrimps where the tip of the third maxillipede or the side of the chela of one of the thoracopods often is used as a shovel for pressing the food lumps into the mouth (see HEEGAARD, 1967). To close the bag anteriorly the antennal scales, which are a pair of large squarish plates, can be bent backwards reaching beyond the mouth opening and thus close the anterior opening of the carapace bag. Besides the ventral and posterior closure of the bag by the first pleopod, the large flat telson plate and uropods can be bent forward by means of the exceptionally strong muscles leading into them, effecting an additional posterior closure of the "carapace bag" with the result that in this position the whole shrimp appears as a closed bulb.

The following four pleopods (Fig. 155) are all placed on a small lobe. The protopod is strong and both exopod and endopod are well developed. All endopods are furnished with an appendix interna. The strongly developed abdomen with well-shaped pleopods caused GURNEY to suggest that *Amphionides* is an adult. This may be true, although neither gonads nor secondary sexual characters are found. From the developmental stage of the pleopods it cannot be a young, larval stage, but from its morphology it may well be a postlarva or an adult.

The uropods (Figs. 156–158) reach a little behind the tip of the telson and are of the usual shape, with the exopod a little stouter than the endopod and with the usual lateral tooth. The uropods have — as the telson — very strongly developed muscles, some of which run directly from the abdomen through the protopod and into the exopod or endopod (Fig. 158).

We have yet to find gonads and sexual characters in *Amphion*. A description of these and the investigation of whether *Amphion* has still further changes in body structure to pass before reaching the sexually ripe shrimp stage are the most desirable achievements to gain in, one must hope, a not too far future.

Gill Formula.

	Mxp ₁	Mxp ₂	Mxp ₃	Pe ₁	Pe ₂	Pe ₃	Pe ₄
Mastigobranchia	1	0	0	0	0	0	0
Phyllobranchia	0	0	1	1	1	1	1

DISCUSSION ON SEX-DIVISION IN AMPHION

Much discussion has taken place about the sexes and the presence or non-presence of gonads in *Amphion*. Gonads were first claimed by DOHRN (1870) later by WILLEMOËS-SUHM (1876), and latest by KOEPPPEL (1902). Now the theory of their presence is practically abandoned. I have made serial sections of an *Amphion* Mysis XIII and was not able to find either mature or embryonic gonad tissue in any of the sections. However, it must be admitted that the material was old and therefore not in the best state of preservation. The shape of the pleopods has been used as a secondary sexual character most recently by GURNEY (1936, 1942) and thus stage XII in this paper should be the future males, because the first pleopod is unbranched (Fig. 98), consisting only of protopod and exopod, while stage XIII and Postlarva I should represent the females of *Amphion* and *Amphionides*, respectively, because the first pleopod is branched (Figs. 99, 128) with both an exopod and an endopod. But as discussed in this paper these are only developmental stages.

Starting with the pleopods of Mysis X (Fig. 80), the first stage with pleopods present, all five are present but only as small undivided, equal buds. In the following stage, Mysis XI, they have developed further (Fig. 90). Pleopods No. 2 to 5 have both exopod and endopod, but the exopod is the largest. In the first pleopod only the exopod is visible and only as a bud-like lobe on the protopod. It can be observed that already this stage shows an anteriorly advancing development with the fifth pleopod the best and the first the least developed. The next in development will be the pleopods of Mysis XII (Fig. 98). Here the pleopods have developed further, but even in pleopods No. 2 to 5 the exopod is still the largest, and in the first pleopod only the exopod is developed and is now of the same length as the exopods of the following pleopods. In the last surface stage, Mysis XIII, a further development has taken place (Fig. 99). The endopods of the pleopods 2 to 5 have each developed an appendix interna, and the first pleopod has developed a small endopod so that all pleopods are now bifurcate.

Parallel to this continuous developmental line in the pleopods is the development of the maxillipedes and pereopods, starting with the maxillipedes in the first larval stage and ending with 5 pereopods in the XIIIth

Table II. Diagram of d

Stage							Mysis
No. of stage	I	II	III	IV	V	VI	
Maxillipedes	1-3	1-3'	1-3	1-3	1-3	1-3	
Pereopods	0	1*	(1)	(1)	1-2*	1-(2)	
Pleopods	0	0	0	0	0	0	
Maxillipede I	2 3 5	2 5 7	2 5 7	2 5 3	2 4 2	2 3 ∞	2
— II	2 4 3	2 5 3	2 4 7	2 4 ∞	2 4 ∞	2 4 ∞	2
— III	2 3 5	2 4 5	2 4 7	2 4 ∞	2 4 ∞	2 4 ∞	2
Pereopod I		(1) 0 0	(1 1 1)	(1 1 1)	2 3 4	2 4 4	2
— II					(1) 0 0	(2 1 1)	2
— III							(1
— IV							
— V							
Pleopod I							
— II							
— III							
— IV							
— V							
Uropod		(1)	1 (1) 1	1 1 1	1 1 1	1 1 1	1
Mastigobranchia on Mxp ₁	0	0	0	0	(1)	(1)	
Pleurobranchia on Mxp ₃	0	0	0	0	0	0	
Pleurobranchia on Pe	0	0	0	0	0	0	
Pairs of telson setae	1-7	1-7	3-7	4-7	(4)-7	5-(7)	

Notes: * = bud-shaped. () = unfunctional or with embryonic, mainly unfunctional, setae. ∞ = more than five joints.

The three figures for maxillipedes, pereopods, pleopods, and uropod are number of joints in protopod, endopod and exopod.

Mysis stage, followed later by a reduction in the abyssal form and by the gradual development of the gills. Firstly, the Mysis V develops the first bud for the coming mastigobranchia on the first maxillipede which only becomes properly functional in the abyssal postlarva. Secondly, the first phyllobranchia-bud appears in the Mysis VIII so that the number of phyllobranchiae has gradually increased to six by Mysis XIII; of these the most posterior one, on the fifth pereopod, only becomes functional in the first postlarval stage just before it again disappears.

Passing from the Mysis stages into the postlarval stages it is interesting to notice how the development of the pleopods continues into the first postlarval stage, so that in the first postlarva the five pairs of pleopods are all fully developed bifurcated appendages with an appendix interna on the endopod.

In addition, the first pleopod has been specially transformed. The endopod is lost in the second postlarva and the exopod fused with the protopod, and in the adult a long uniramous and unjointed organ is shaped. Finally the fifth pereopod, which still existed in the first postlarva as a reduced limb, but for the first time with a fully developed phyllobranchia, is lost in the second postlarva.

The changes occurring in the pereopods, pleopods, and gills with the development from stage to stage are only steps in a continuous gradual development, but without development of any sexual characters. That this only is a non-sexual adaptation for the new abyssal life and no sexual differentiation is also supported by the development and changes in all other organs: antennae, eye, the last adding a luminescent organ to its function, mouth appendages, carapace, and last but not least, the hepatopancreas, which strongly decreases in the abyssal life, probably a degeneration correlated with the scarcity and poor quality of food in this environment.

In the final stage, earlier called *Amphionides valdiviae*, here adult or Postlarva III of *Amphion reynaudi*, we find no sexual characters. I have called it adult or Postlarva III because, although it most likely is the adult, we cannot know this for certain as long as no sexual characters either gonads or external characters have differentiated. Here it can also be noted that the luminescent organ connected with the eye is found in all adults and in development in the three specimens of Postlarva II, and therefore cannot be interpreted as a male character. Possibly it helps the specimens of both sexes to find each other, besides functioning in the search for food and for attracting organisms with light perceptive organs.

Diagram of development.

I	Mysis							Postlarva		Adult
	VII	VIII	IX	X	XI	XII	XIII	I	II	
3	1-3	1-3	1-3	1-3	1-3	1-3	1-3	1-3	1-3	1-3
2)	1-2	1-(3)	1-4*	1-4	1-4	1-4	1-5	1-5	1-4	(1) 2 (3-4)
	0	0	0	1*-5*	(1-5)	(1-5)	(1-5)	1-5	(1) 2-5	1 2-5
∞	2 3 ∞	2 3 ∞	2 3 ∞	2 3 ∞	2 3 ∞	2 3 ∞	2 3 ∞	2 3 ∞	2 3 ∞	2 5 5
∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	(2 4 1)	(1 1 1)
∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	(2 4 ∞)	(1 3 1)
4	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	(2 4 4)	(2 4 1)
1)	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 5 (∞)	2 5 (3)
	(1) 0 0	(2 1 1)	2 4 4	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	2 4 ∞	(2 5 3)	(2 5 3)
			(1) 0 0	2 4 2	2 4 ∞	2 4 ∞	2 4 ∞	2 0 ∞	(2 4 3)	(2 4 3)
									0 0 0	0 0 0
				(1)* 0 0	(1 0 1)	(1 0 1)	(1 1 1)	1 1 1	(1 0 3)	1 0 1
				(1)* 0 0	(1 1 1)	(1 1 1)	(1 1 1)	1 1 1	1 1 1	1 1 1
				(1)* 0 0	(1 1 1)	(1 1 2)	(1 1 1)	1 1 1	1 1 1	1 1 1
				(1)* 0 0	(1 1 1)	(1 1 1)	(1 1 1)	1 1 1	1 1 1	1 1 1
				(1)* 0 0	(1 1 1)	(1 1 2)	(1 1 2)	1 1 1	1 1 1	1 1 1
1	1 1 1	1 1 1	1 1 1	1 1 1	1 1 1	1 1 1	1 1 1	1 1 1	1 1 1	1 1 1
	(1)	(1)	(1)	1	1	1	1	1	1	1
	0	1*	1*	(1)	(1)	1	1	1	1	1
	0	0	1*	(1)-2*	1 (2) 3*	1-3	1-3+(4-5)	1-5	1-4	1-4
7)	5-6	(5)-6	(5)-6	5*-6	(6)	6	0	(1)	(1)	(1)

SUMMARY OF DEVELOPMENT AND GROWTH

Figs. 159-165. Tables III-V.

In the chapter on distribution it will be shown that the Mysis larvae live in the surface layers of the ocean down to about 30-40 m, at least by night when most of the hauls have been taken. That *Amphionides valdiviae*, as shown in this paper, is the adult of *Amphion* fits well with the fact that GURNEY (1942, p. 223) has taken a specimen of the first larval stage from deep water at Bermuda. Under Promysis (p. 10) it is mentioned that GURNEY has possibly overlooked the rostrum because it either was bent in around the metope or, less likely, not yet developed. GURNEY'S stage must have been the Promysis stage. Presumably spawning takes place at 2000-5000 m and often in places where there is a further distance to the bottom. It must therefore be expected that the eggs have a specific gravity a little lower than that of the sea water or through respiratory products during development receive an updrift so that they slowly will rise to the surface, during which journey hatching takes place. This will explain why a Promysis was caught in deep water as well as the fact that all the Mysis stages are found near the surface.

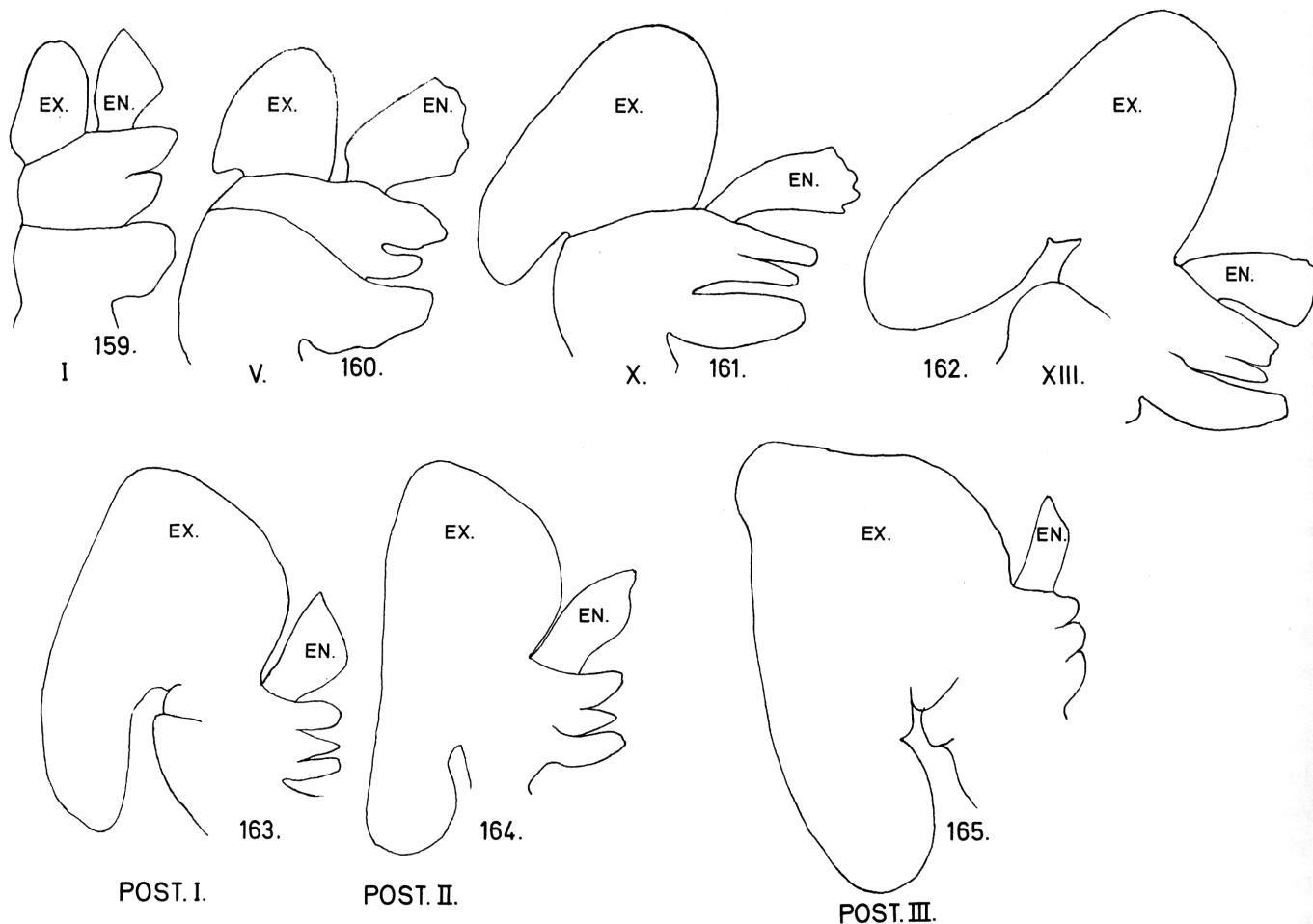
From Tables XII-XIV can be seen that the different larval stages are found throughout the year. We must therefore assume that spawning takes place throughout the year without any larger seasonal break.

It is shown in text and figures that 13 Mysis stages exist, (see the summary in Table II). From this it appears that the larva starts with two antennae, mandible, maxillula and maxilla and three maxillipedes of which the second and third maxillipedes are the locomotory organs. But already in the second Mysis the first pereopod starts to develop as a little bud. From then on the pereopods are developed successively until Mysis XIII, which has all five pairs of pereopods, only the fifth pereopod never develops an endopod, and the exopod of this limb functions as an endopod. This sounds contradictory, but must be understood from the fact that if there is a difference in time of development of exopod and endopod, in the Crustacea it is always the exopod which develops first. In this case there is no absolute use for an exopod on the last pereopod, but instead for a posterior closure of the endopodial catching basket shaped by maxillipedes (except the first) and pereopods. With this purpose the extraordinary case is found that the exopod on the fifth pereopod in this single stage is shaped like the anteriorly situated endopods and also functions as an endopod. It is of further interest to note that this limb remains in the first postlarva but is nonfunctional and is missing in the second postlarva and the adult. Furthermore its pleurobranchia is bud-shaped in the last Mysis stage, developed to function in the first postlarva where the limb itself has become vestigial, and again both limb and gill are lost from the second postlarva.

A further point of interest in the development is the number of endopodial joints. In the first maxillipede they increase from three to the normal number of five in the second Mysis. But already in the fifth Mysis joints number two and three fuse, resulting in a total number of four. In the following stage, Mysis VI, this is reduced to three, through a fusion into one joint of the original fourth and fifth joints. From here on the endopod remains with three joints, up to the adult in which we again find the full number of five endopodial joints.

In the second maxillipede the four endopodial joints of the first Mysis add a fifth joint in the second Mysis. This fifth joint is lost again in the following stage. Another point of interest is that in the third maxillipede and all five pereopods the number of endopodial joints is never more than four beginning with the stage when the limbs have reached full development and continuing throughout all the Mysis stages. It is first in the adult that the pereopods number two and three develop five endopodial joints. The remaining limbs are left with four or fewer endopodial joints. For the second pereopod this is easily understandable because this limb in the adult has developed into the peculiar piston-shaped organ described under the adult. But that the following third pereopod also has developed a fifth joint in the adult stage is more surprising as this limb is vestigial. It looks as if some of the developmental hormones for the second pereopod have penetrated into the third pereopod, also as it — although nonfunctional — is the largest of the vestigial appendages.

This number of four endopodial joints in the pereopods of the larval form shows an interesting analogy



Figs. 159–165. *Amphion reynaudi*, second maxilla. The development and transformations of the second maxilla are shown through the larval life. The Roman numerals under the first four figures indicate the number of Mysis stage to which it belongs. The three last figures are from Postlarva I and II and Postlarva III or adult as I also have called it in some places.

with the Phyllosoma larva where also only four endopodial joints are found in the pereopods, while the adult Scyllaridae have the normal five endopodial joints.

Further, it has been pointed out that the second and third maxillipedes are built like, functions as, and follow in development the following pereopods, and that there is a larger interval in the placement of the first and the second maxillipedes than between any other of the appendages. This is the same as in the Euphausiids and could with right be interpreted as this shrimp having only one pair of maxillipedes contrary to all other Eudecapoda. But whichever way it is interpreted it definitely shows a remarkably primitive character. Other interesting points in the development are that the metope is extremely well-developed — normally it is missing in higher Crustacea — and that the development of both the incisor and the molar teeth of the mandible shows clearly that they are transformed plumose setae, the latter is in no way surprising, but it has — as far as I know — never been noticed before. It must here be understood that a development like this cannot be special for *Amphion* but must hold true for the mandibles in all Crustacea. The second maxilla has an interesting functional development. It starts as a typical copepodal swimming limb (Fig. 159). The exopod then develops first its posterior, later its anterior lobe, and at the same time the endopod turns 90° in a medial direction in order to be able to function as a masticatory endite (Figs. 160–162). In the postlarva and further in the adult the anterior lobe of the exopod even enlarges, but the endopod decreases in size into a non-functional and vestigial organ, and at the same time it turns back into its original longitudinal axis. Simultaneously with these changes the three protopodial endites decrease in size nearly to the point of disappearing (Figs. 163–165).