In the first maxillipede (Fig. 78) the coxa is only a small stalk with a sausage-shaped epipodite, the mastigobranchia. The endite of basale has further developed to a large masticatory plate lined with plumose setae. The endopod is three-jointed and the first and shortest joint has a small masticatory process and a large number of plumose setae of only half the length of the relatively fewer setae in stage VI. The exopod is a long lash with the first and the last joints clearly set off from the rest and some not clearly delimited joints in between. Plumose setae are found only on the more distal part. As the limb is placed along the side of the mouth reaching forward to the labrum, it seems to function partly for bringing food particles into the mouth, partly as a lateral bar of the mouth region.

The first and second maxillipedes are widely separated, and as second and third maxillipedes have a true thoracal function, one could — if *Amphion* was not a decapod — say that the species had only one pair of maxillipedes. At least the second and third maxillipedes, together with the thoracopods, form the catching basket of the larva, and their exopods function as swimmerets. Of the thoracopods or pereiopods, no. 4 (Fig. 79) is the last developed and functions to close the catching basket posteriorly. It is only half the length of the anteriorly placed thoracopods. The pleurobranchiae of third maxillipede and first pereiopod have grown but are still compact in shape and unbranched. A small gill-bud has developed at the base of the second pereiopod behind the two other gills.

All five abdominal segments have developed pleopods as small buds with the basal half covered by the abdominal pleurae which now are sticking out free from the abdomen.

Dimensions.

Total length 13 mm; length of carapace 7 mm; width of same 2 mm; rostrum 0.2 mm; abdomen 4 mm; telson 2 mm.

## Mysis XI

Figs. 81–90.

*Development.*

The medial part of the frontal margin of the carapace between the two orbital spines is pushed forward, and both thorax and abdomen are enlarged. The telson plate has lost the vestigial setae no. 5, and no. 6 is very short. The first antenna and the pleopods show a varying development (Figs. 85 and 86) because the individual variation becomes more outspoken in older stages added up from previous smaller variations. The locomotory limbs have developed spines and stiff setae on the endopod for catching purposes (Fig. 89). The gills on maxillipede no. 3 and pereiopods 1 and 2 have grown to functional size, that on the first pereiopod is the best developed. A gill bud has appeared at the base of the third pereiopod. The pleopods have developed from a mere bud into a protopod with leaf-shaped exo- and endopods. In the group with well-developed first antenna, only the first pleopod is missing the endopod. Especially the abdomen and telson have grown considerably in size from the previous stage.

Thorax.

The thorax has grown in length and width, and the part between the orbital spines reaches farther anteriorly.

Abdomen.

The abdomen has enlarged, and the ventral free part of the lateral pleura is further developed. The development is in this stage concentrated on the abdomen and telson rather than on the thorax region as in the previous stages.

Telson.

On the telson the setae no. 6 are still shorter, placed at the tip of the telson as two small spines. The fifth setae, which in the previous stage were small dots, are now intirely lost. In some specimens the telson is a little

more pointed and the two spines are a little shorter than in others (see Figs. 82, 83). The telson plate is about twice as long as in the previous stage.

Appendages.

Although there is a large variation in size of the eggs taken from the abdomen of a decapod female, this varation does not show so distinctly in the larvae when the larval development is limited to two or three Zoëa-Mysis stages, as is the general rule in decapod larvae. However, if the larval life is increased by several more stages, the differences among larvae of even the same brood add up from stage to stage, so much that in the later larval stages a considerable difference between the specimens within the same stage is found. This was clearly and most admirably shown by FRASER (1937), who reduced the nearly 30 stages described in Euphausids to 12 larval stages, including three Nauplius stages for *Euphausia superba*. A similar variation is found here in *Amphion* where the number of larval stages also is numerous, 13 plus some postlarval stages.

HEEGAARD (1966) showed for the oceanic Penaeids that the larval life was more extended in species spending a larger part of their development in the open ocean than in species living nearer to the continents or on the shelf itself. This prolonged larval life was explained as caused by a poorer nutrition in the open ocean than closer to the coast, and by the fact that species with an adult life in deeper regions of the ocean grow to a larger size before changing into the adult and penetrating into the deeper water layers than those species of which the adult life takes place on or near the shelf in more shallow water. It is therefore in line with this view that *Amphion* as a true oceanic pelagic form shows a much prolonged larval life, first as the well-known *Amphion* larvae among the plankton in the uppermost layers of the sea and later, as we shall see, penetrating down into some thousand meters depth where it changes considerably into a postlarval form and where we must expect to find also the adult, if the largest known stage not is the adult.

In line with this, when reaching the XIth Mysis stage, we therefore find that certain morphological differences exist between the larvae belonging to this stage. This is especially the case in development of the first antennae, the gills, and the pleopods.

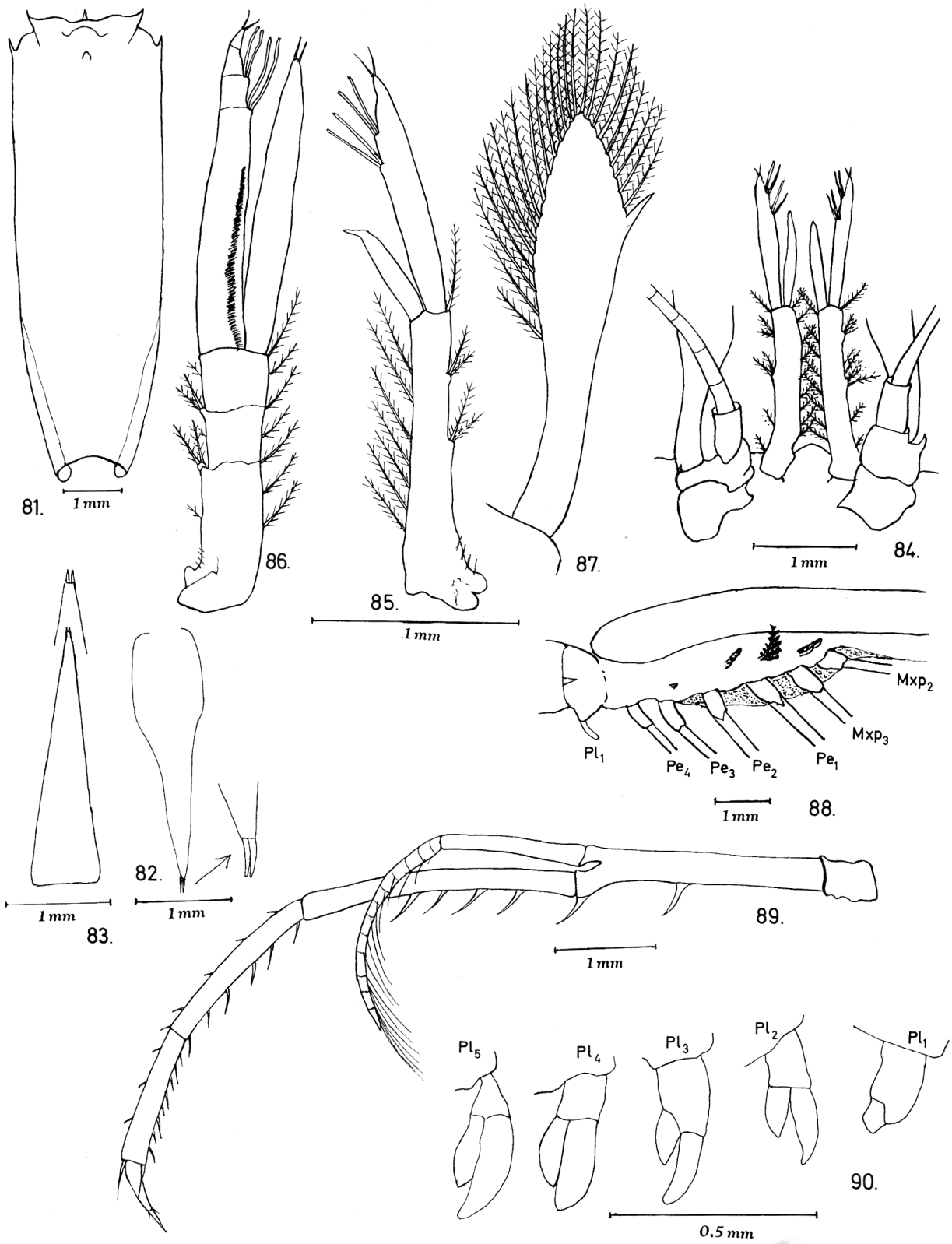
In the least-developed larvae only little change from the previous stage has taken place in the first antenna (Fig. 85); it is a little stouter, the two groups of setae on the lateral side of the stem are stiff, plumose spines, and further on the medial side of the lateral flagellum two groups each of two aesthetascs are developed in the distal third of its length. The medial flagellum is still small, only half the length of the lateral one, and both are unjointed.

In the advanced larvae the first antenna (Fig. 86) is more developed. The whole antenna is stouter and the stem is divided into three joints or only nearly so, because there is not yet a very clear line across the stem in line with the two lateral groups of spiny setae. The lateral flagellum is also beginning to be divided into joints from the proximal group of aesthetascs to the tip. Further, a dark string is running through the proximal half near the medial margin, but under the cuticle. The long preservation makes the material unfit for a more complete examination. The medial flagellum is in these larvae nearly as long as the lateral, but always unjointed as in the previously described larva. It should be stressed that although the antennae seem to indicate different developmental stages, the total length of the larva is the same in both groups, and that intermediate developmental stages are present in the material.

In the second antenna the coxa seems to have widened a little and the hook on the distolateral corner of basale is larger. The antennal scale is still characteristically long, stilet-shaped, with its basal part developed as a long shaft.

For the mouth appendages it can be noted that the posterior lobe of the exopod of the second maxilla has grown, as have the masticatory endite on basale and the mastigobranchia from the coxa of the first maxillipede.

The locomotory and prey-catching limbs, from second maxillipede to the fourth pereiopod, have developed further, both their exopodial swimming branch as well as the protopodial and endopodial catching basket, the third maxillipede has two thorny spines on the basale and four on the first endopodial joint. The two following joints are lined with long, stiff setae (Fig. 89), and together with a terminal short spine, the last joint forms a curved claw. Characteristic for *Amphion* is that the endopods on all maxillipedes and thoracopods




Figs. 81–90. *Amphion reynaudi*, Mysis XI. Fig. 81, carapace from dorsal, giving place of metope and anterior dorsal organ. — Figs. 82–83, telson plate. — Fig. 84, first and second antenna from ventral showing anterior border of carapace and metope. — Fig. 85, right first antenna from dorsal. — Fig. 86, another developmental form of this stage, left first antenna from dorsal. — Fig. 87, antennal scale of right second antenna. — Fig. 88, posterior part of thorax and anterior part of abdomen showing gills, proximal part of limbs and lateral process. — Fig. 89, third maxillipede. — Fig. 90, first to fifth pleopod.

have only four joints against the normal five joints. This description of the third maxillipede covers all the basket-limbs except the second maxillipede and the fourth pereiopod, which are placed anteriorly and posteriorly in the basket and are a little shorter than the rest, with fewer spines and setae.

The gills on the third maxillipede and first and second pereiopods have developed to functional size. In the least developed larvae (Fig. 88) the gill on the first pereiopod has free lateral branches on the stem, like the rami of a feather. The gills on third maxillipede and second pereiopod have not developed so far but look more like a foxtail. A gill-bud is seen on the third pereiopod. In the more advanced specimens all three first gills are feather-shaped, but the gill on the third pereiopod is also here only a bud.

Also the pleopods are differently developed in the larvae of this stage. In some larvae we find an unjointed protopod with a leaf-shaped exopod and endopod, the exopod being always the largest. Only in the first pleopod is the exopod just a small bud on the end of the protopod, and the endopod has not yet developed.

In the more advanced larvae both the protopod and its exopodial and endopodial branches are better developed, but the first pleopod is also here without the endopod and has only begun to develop the exopod (Fig. 90). It is of interest to note that the most posterior pleopods develop first, so that number five is the best developed, number one the least. A similar, but not so pronounced, difference in development is noticed in the Stenopidea and in Leptochela (GURNEY 1936, GURNEY and LEBOUR 1941) if one is to judge from the descriptions.

The uropod is almost fully developed, with the endopodial leaf reaching the tip of telson and the exopod somewhat farther; the exopod has a strong lateral spine.

Dimensions.

Total length 17 mm; length of carapace 8 mm; width of same 3 mm; rostrum 0.3 mm; abdomen 6 mm; telson 2.5 mm.

## Mysis XII

Figs. 91–94, 96–98.

*Development.*

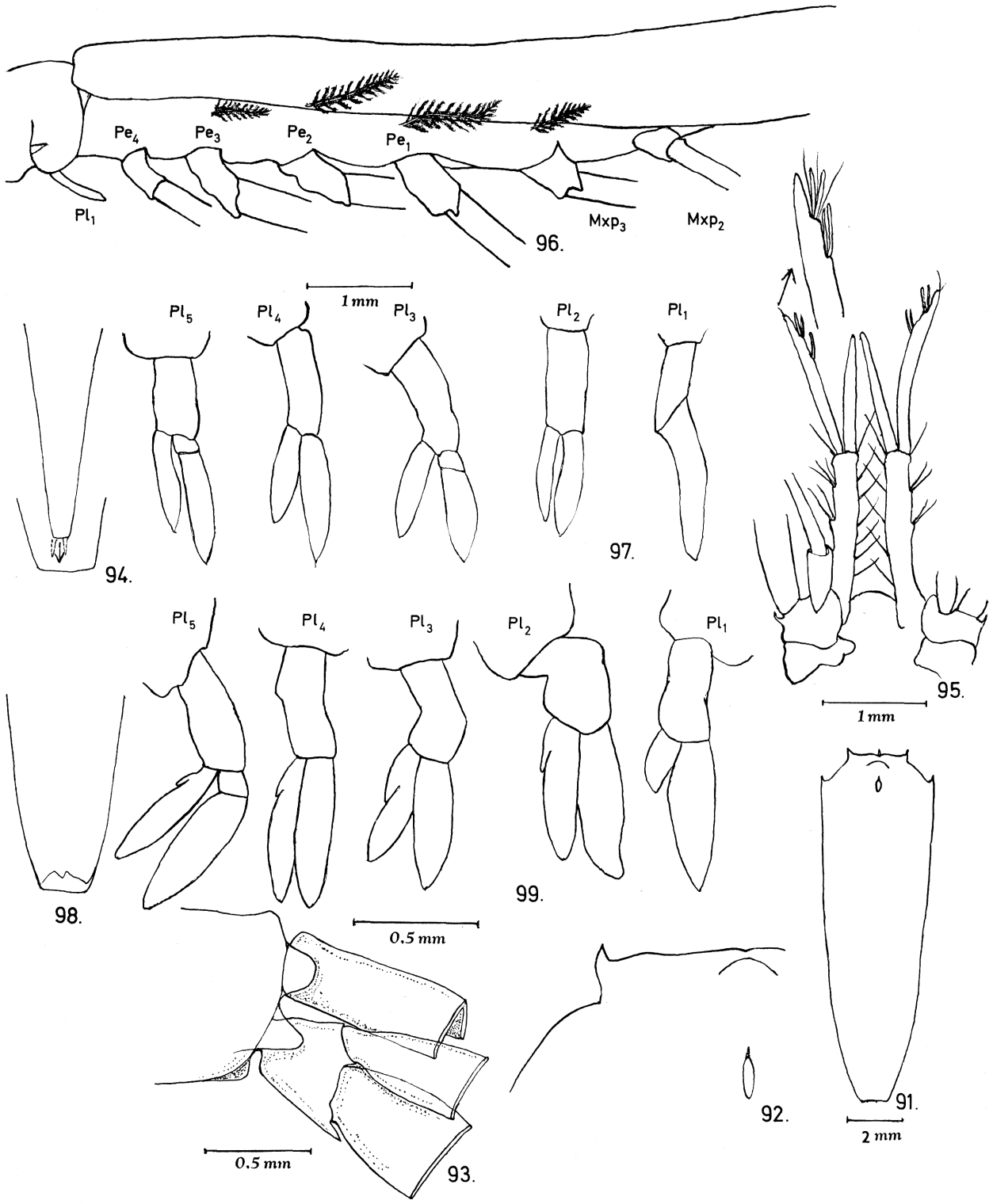
From stage X to XI especially the abdomen became enlarged, but from XI to XII again both the thorax and abdomen show the main part of the enlargement. The anterior dorsal organ is pointed anteriorly with a short spine. The fourth pereiopod reaches nearly the size of the preceding ones. The number of gills is still four, but they are all feather-shaped, branched and of functional shape and size. The pleopods have enlarged, first pleopod is without endopod, and some of the least-developed pleopods show a beginning division of the protopod into two parts. The tip of the telson plate is square-cut and bears a vestigial pair of short setae, the original large pair no. 6.

Thorax.

The thorax and its carapace have again started to grow in length, and the carapace has become much wider anteriorly, from about 2.5 mm to 4 mm between the antennal spines. These spines are pushed further posteriorly, so judging only from these older stages, the spines could be called branchiostegal spines, but their position in the youngest stages shows them to be antennal spines. Posteriorly from these spines the carapace tapers slowly and lacks the more parallel lines earlier present in the anterior half. The delicate rostrum is often broken. The anterior dorsal organ has become elliptical and is anteriorly continued as a short, conical spine (Fig. 92). This may indicate that — as known also from some other decapod larvae — the anterior dorsal organ in older stages may be replaced by a spiny bulb or short ridge.

Abdomen.

The free ventral part of the lateral pleurae has grown, forming on each side a line of stabilizing keels between which the pleopods are placed. On each side of the sixth segment are developed two pleural plates (Fig. 93). The dorsal one covers the base of the telson plate, the other is placed laterally of the base of the uropod. A short unpaired longitudinal keel is found ventrally, in front of the anus.




Figs. 91–97. *Amphion reynaudi*, Mysis XII. Fig. 91, carapace from dorsal. — Fig. 92, left anterior part of carapace showing orbital spine, anterior dorsal organ with beginning frontal spine, and metope. — Fig. 93, part of sixth abdominal segment with ventral keel and lamellar processes at the base of telson and uropod. — Fig. 94, telson plate. — Fig. 95, part of first and second antenna from ventral — Fig. 96, posterior part of thorax and anterior part of abdomen with gills, lateral process of abdomen and proximal part of limbs. — Fig. 97, first to fifth pleopods.

Figs. 98–99. *Amphion reynaudi*, Mysis XIII. Fig. 98, distal part of telson. — Fig. 99, first to fifth pleopod.

Telson.

The telson plate tapers more strongly posteriorly (Fig. 94). Its tip is square-cut and bears the very vestigial setae no. 6. They are often broken as indicated by the stipled line in the figure, but a scar shows clearly where they were placed.

Appendages.

The mouth-appendages and the thoracopods have not developed much from the previous stage. The first and second antenna and the mandible are nearly unchanged. The endopod of the first maxilla has through the stages been gradually reduced and turned from an anteriorly to a more medially pointing direction at the same time as it more and more, together with its two endites, takes on the function of a third masticatory process. In the second maxilla it is especially the posterior lobe of the exopod or scaphognath which is developing, so much so that one can hardly imagine that it was entirely missing in the early stages. The masticatory process on the basale of the first maxillipede has enlarged little by little through the stages and is now of a considerable size. Also the exopod has grown, but the endopod has been reduced except that the basal joint forms a small masticatory process. On the following thoracic limbs the exopodial swimmerets have grown and the endopods have become more and more spiny and hairy, shaping a perfect trap or catching basket for smaller plankton organisms. The last, fourth, pereiopod is now nearly as large as the preceding one. Of the fifth pereiopod nothing is seen.

The pleurobranchiae are still only four, excluding the mastigobranchia on the first maxillipede, and placed at the base of the appendages from the third maxillipede to the third pereiopod. Thus the second maxillipede and the fourth pereiopod are without gills. The four gills on the thorax have all grown into long, feather-shaped organs pointing from their base forward under the carapace (Fig. 97).

The five pleopods have grown further from stage XI with both longer protopods, exopods, and endopods. The first pleopod has only an exopod but no endopod. All the others have both exopod and endopod (Fig. 98). In some specimens the exopod of the third and fifth pleopod is divided into a short basal and a longer distal part, in others not. No setae were seen on the pleopods, except sometimes a delicate setal hair at the tip of either exopod or endopod.

In the uropod a hooked spine has developed on the distolateral corner of the protopod (Fig. 93).

Dimensions.

Total length 23 mm; length of carapace 13 mm; width of same 4 mm; rostrum 0.3 mm; abdomen 8 mm; telson 2.5 mm.

## Mysis XIII

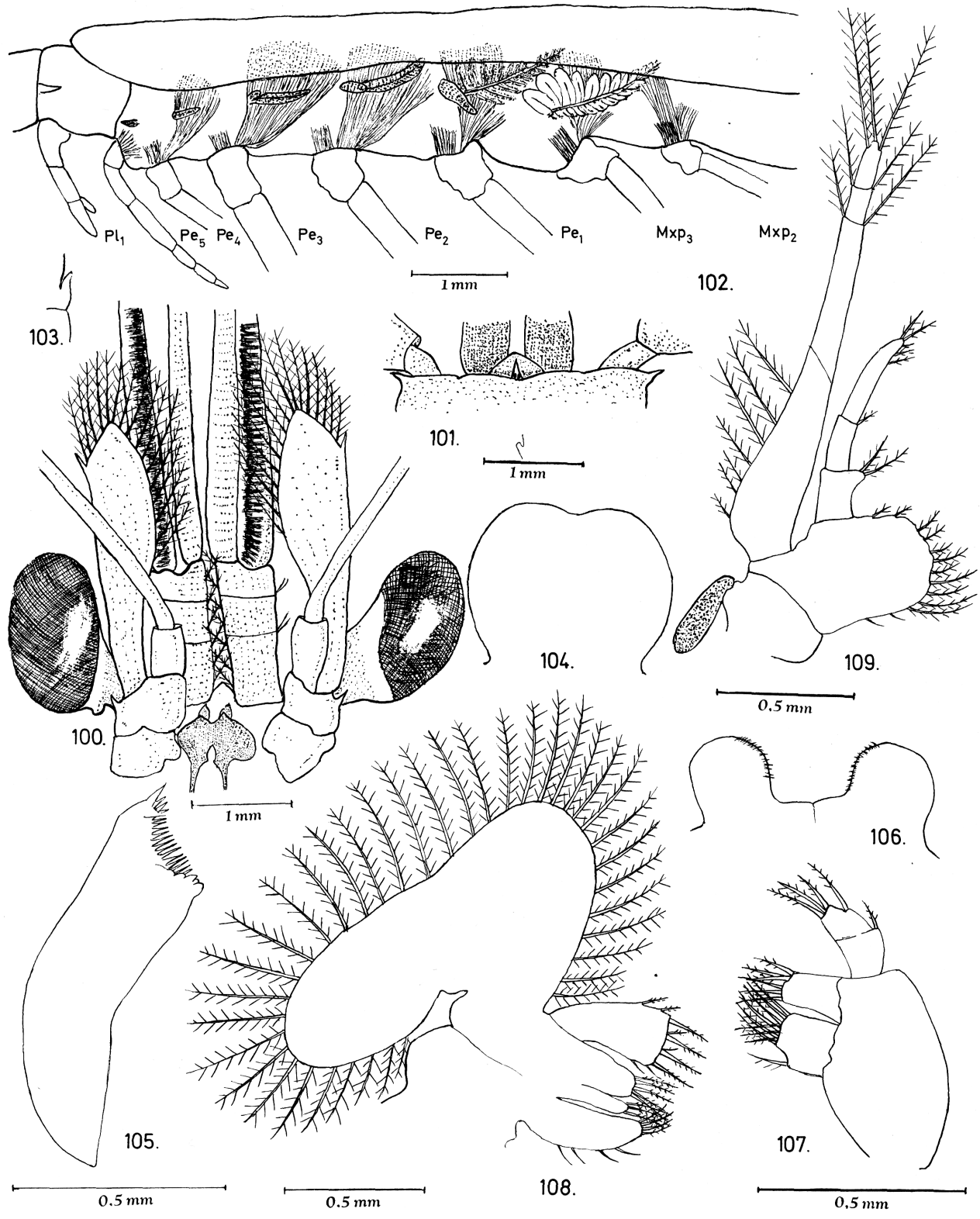
Figs. 95, 99–116.

*Development.*

Both thorax and abdomen have grown. The anterior dorsal organ and its anterior projecting spine have enlarged (Fig. 110). The fourth pereiopod is nearly as large as the preceding ones and an unbranched fifth pereiopod with a two-jointed protopod and a several-jointed exopod has developed. (Fig. 116). The gills have increased from 4 to 6 by gill-buds on the fourth and fifth pereiopods. The pleopods have enlarged. All five have both exopod and endopod and, except for the first one, an appendix interna. The telson plate is square-cut posteriorly, (Fig. 95) either without or with vestigial pins of the sixth setae. (Fig. 114).

Thorax.

The thorax and carapace have again started to grow. Some of the specimens can be much larger than the average and have a carapace widening posteriorly, as the one figured in Fig. 110. Of course the higher the number of the larval stage the larger is the variation in size and development. The anterior dorsal organ is elliptical with a longitudinal crista and a spine pointing anteriorly (Figs. 110 and 111, drawn from an Atlantic specimen showing both rostrum and anterior dorsal organ with anterior pointing spine or postrostral spine).




Figs. 100–109. *Amphion reynaudi*, Mysis XIII. Fig. 100, anterior part of thorax from ventral with brain, dorsal and ventral frontal organs, metope, first and second antenna and eye. — Fig. 101, frontal part of thorax from dorsal showing frontal margin of carapace with orbital spines, rostrum, metope, nauplius eye and anterior dorsal organ, further proximal part of first antenna and eye stalk. — Fig. 102, posterior part of thorax and first abdominal segment, the latter with first pleopod and lateral process. Thorax with part of carapace, gills and proximal part of limbs. — Fig. 103, lateral process of first abdominal segment from dorsal. — Fig. 104, labrum. — Fig. 105, mandible. — Fig. 106, labium. — Figs. 107–108, first and second maxilla. — Fig. 109, first maxillipede.

The orbital and antennal spines are still present in this surface stage and are even larger than in any earlier stage.

From the brain the paired dorsal frontal organ extends forward (Fig. 100 shows the anterior part of the larva seen from ventral). Behind the dorsal frontal organ and more ventrally are seen the two much smaller lobes of the ventral frontal organ. Between these lobes the unpaired ventral or medial nauplius eye may be found, but it was not visible on any of the examined specimens. The nauplius eye, which often is small and unpigmented, has in some copepods like Trebinae and Saphirinae moved to the dorsal surface and is placed between or posteriorly of the paired dorsal nauplius eyes and is in such cases supplied with a lens.

Between the lobes of the dorsal frontal organ the double nauplius eye is found (Fig. 101). It is placed inside the brain, on its dorsal surface, and with its two eyecups very close together, but not touching each other with their back walls. It is in all stages without a lens. In front of the brain the metope can still be seen (Fig. 100) under the rostrum (Fig. 101).

Abdomen.

The abdomen is longer. The free parts of the lateral pleurae have grown as described for stage XII. The lateral process on the first abdominal segment (Fig. 103), which was present already in the first Mysis stage to prevent the carapace from sliding backwards, still exists and has now also to prevent the carapace from pressing on the gills. Both functions have the purpose of ensuring the free access of water to the respiratory membranes under the carapace or on the gills. The pleurae and the sixth abdominal segment with its ventral keel are equal in stages XII and XIII.

*Telson.*

The telson plate is developed as in XII, only more often the no. 6 spine is entirely missing and the telson square-cut. In some specimens the developing cuticle of the telson could be seen under the existing one (Fig. 95), with a pointed tongue in the middle of a shallow cleft. The shallow cleft will disappear during the ecdysis due to inner pressure and following enlargement. The lateral sides will be more straight, ending in the point which before the ecdysis was pressed backwards inside the tube of the telson. In other specimens the telson may have not only vestigial parts of the sixth setae but also scars from where setae nos. 5 and 4 were placed (Fig. 114).

Appendages.

As mentioned for previous stages, the first antenna was stouter in some specimens than in others, but no other explanation than growth variation could be found. In the best developed specimens, stage XI, the peduncle of the first antenna is divided into three joints. The first is a little longer than the two following, which are of about equal length. Comparing the first antenna of Mysis XI and XIII (Figs. 86 and 113) it can be seen that the peduncle of the antenna is only a little longer in stage XIII, but stouter. The diameter has grown from $^1/_4$ mm to more than $^1/_2$ mm. The armature of setae on the peduncle is about unchanged in the three stages. However, the two flagella have changed. The medial has grown about $1^1/_2$ mm in length to over 3 mm, and the lateral flagellum also reaches 3 mm. The lateral flagellum is as in the previous stage divided into four joints of which the first is more than twice the length of the three following together, and the same two aesthetascs are present medially at the end of the first and second joints.

In the basal joint, for the first two thirds of its length, a dark "string" was seen in some specimens of stage XI. This string now runs through both the first and second joints in their full length. (Figs. 100, 113). The string is pressed more towards the medial margin, but from it small parallel lobes have developed towards the lateral margin. It is difficult to say anything definite about this organ due to the great length of time the material has been preserved, but it reminds one very much of embryonic olfactory organs, which are fully developed in a later stage.

The second antenna has not changed except for growth in size, as the rest of the larva. The exopodial antennal scale is still remarkably elongated with its basal part as a long stalk and the distal plate narrow and elliptical with a pointed tip.

The labrum (Fig. 104) is a circular plate with low incision medially on its free margin; no setae were found on its free margin. The mandible (Figs. 105, 115) has developed into a powerful organ with a comparatively larger and more elongate corpus mandibulae than in Mysis X. The primary incisor teeth have become more pushed together as a small group at the distolateral corner. Between these and the molar teeth at the mediolateral corner is a sharp ridge with a single line of secondary incisor teeth. In Mysis X (Fig. 74) these teeth were movable at the base so that when used they could yield to the pressure and not break. But in this XIIIth Mysis stage (Fig. 115) their bases have become chitinized immovably to the edge, and they must now be strong enough for not breaking when in use. The mandible is still without a palp.

The labium (Fig. 106) is wide at the base with two short, rounded lobes furnished on their medial margin with a few short, stiff hairs.

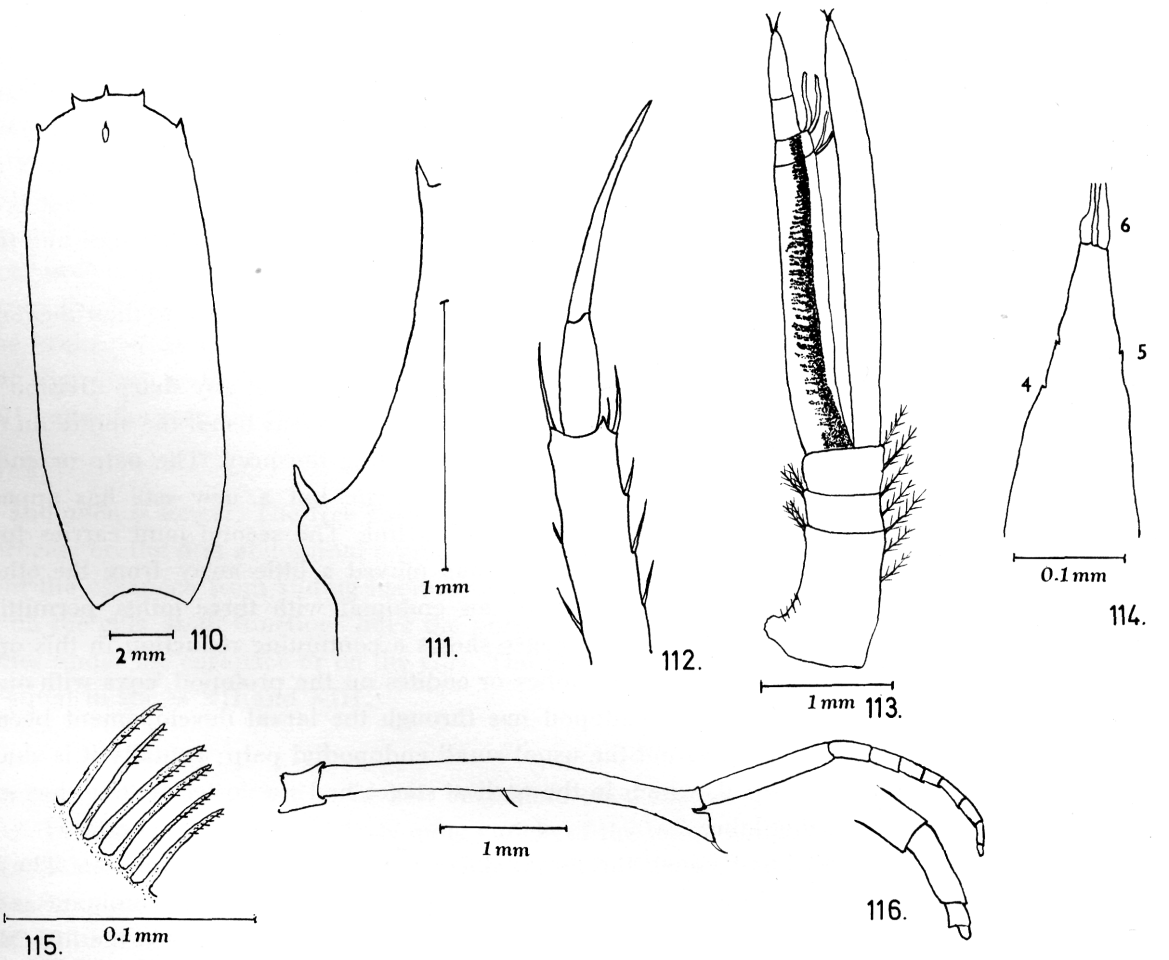
The first maxilla (Fig. 107) has developed a stout elliptical protopod without any sharp division between coxa and basale. The two endites remain and are placed close together, and as usual the spines on the basiendite are the strongest and can be used as secondary teeth for cutting the prey. The palp or endopod is divided into two joints although no movability exists between them, but a new seta has appeared on the distolateral corner of the first joint to mark the demarcation line. The second joint carries four setae of which the fourth was added in the fifth Mysis: now it has moved a little away from the other three and this may indicate that the following stage will show an endopod with three joints, permitting it to function as a palp, but on the contrary the postlarval stages shows a continuing reduction in this organ.

The second maxilla (Fig. 107) has still only three lobes or endites on the protopod, coxa with one single, and basale with the usual two. The unjointed endopod has through the larval developement been turned more and more medially and therefore it has not the usual small endopodial palp; actually it is shaped and functioning as a fourth endite. The exopod, which in the earliest stages had no posterior lobe, has gradually developed a large, backwards pointing lobe.

The first maxillipede (Fig. 109) has through the larval stages developed two gnathobases. The first one is nearly the whole basale, which is pointing medially as a large lobe and is the more prominant as the coxa is almost reduced to a basal peduncle. The exite on the coxa which first was observed in the fifth Mysis has developed into a sausage-shaped mastigobranchia pointing backwards, i.e. towards the basis of the limb. The second much smaller gnathobase is developed from the first endopodial joint, as a small lobe with two distomedial setae. After the first joint follows a second of about the same length, tipped with a single distomedially placed seta. The third joint is twice as long as each of the two previous joints. As we have seen in Mysis V both the second and the third joints have been formed by a fusion of the two joints. On the exopod the first joint has developed a lateral ridge with a line of plumose setae at its crest: these setae possibly function as an undulating fan for drawing the water current forward from under the carapace. The rest of the exopod is a long three-jointed stick which in Fig. 109 is drawn straight, but in reality usually is bent ventrally at the tip. As it reaches forward beyond the mandibles and the mouth opening it seems to function partly for carrying prey particles to the mouth, partly for cleaning the mouth-appendages. The first and second joints in the exopod are very long, the two following joints rather short.

The second and third maxillipedes still do not function as true maxillipedes but both are in shape and function entirely as the following thoracopods: they have well-developed exopodial swimmerets and an endopodial "walking" branch, which, due to the entirely planktonic life, are not used for walking but for forming the catching basket, especially its finer network. The larva is furnished with the many thorns, spines, and stiff setae along the protopod and the endopod, as described under Mysis (Fig. 89). To this is now added the growth of the distal claw into a long sickleshaped organ (Fig. 112).

The fifth thoracopod (Fig. 116), not found in stage XII, is now a delicate limb less than half the length of the preceding ones and without an endopod. From the figure it could appear as if an endopod had been lost, but no scar at the end of the protopod indicates this. It is of interest to notice this lack of an endopod because all the other thoracopods are — in a much earlier developmental stage — not only clearly bifurcate, but their endopods are better developed than their exopods. As can be seen from studying the different stages, the presence of this fifth thoracopod is only a natural link in a developmental series in which the most posterior




Figs. 110–116. *Amphion reynaudi*, Mysis XIII. Fig. 110, carapace from dorsal with rostrum, orbital and antennal spine, and anterior dorsal organ. — Fig. 111, rostrum and anterior dorsal organ from lateral in their natural position on carapace. — Fig. 112, distal tip of second pereiopod. — Fig. 113, left first antenna from dorsal. — Fig. 114, telson plate as seen in some specimens (see text). — Fig. 115, secondary incisor teeth of mandible. — Fig. 116, fifth pereiopod with tip of exopod.

units develop first. It has nothing to do with a secondary female character as it was interpreted by ZIMMER (1904) and GURNEY (1936, 1942).

The pleopods (Fig. 99) are now all developed as bifurcated appendages. All endopods except that of the first pleopod have developed an appendix interna, and on the fifth pleopod the exopod has a short basal joint as is common for some decapods. Finally, the first pleopod has developed an endopod which is still rather short. In Mysis XII the pleopods have begun their bifurcation. Normally in Decapoda this takes place from the first to the fifth pleopod, but in *Amphion* — as mentioned above under Mysis XII — the development of the pleopods proceeds from the fifth to the first. Because the first pleopod is the last to develop, it is in Mysis XII, contrary to what is the condition in the following pleopods, still unbranched without an endopod. In Mysis XIII all pleopods have become bifurcate. This GURNEY (1936) (1942) misinterpreted, considering Mysis XII as a future male because of the unbranched first pleopod and Mysis XIII, in which the same limb now is bifurcate, as a future female.

For the uropods no differences were observed between this and the previous stage.

Dimensions.

Total length 25 mm; length of carapace 14 mm; width of same 4.5 mm; rostrum 0.3 mm; abdomen 9 mm; telson 2.5 mm.