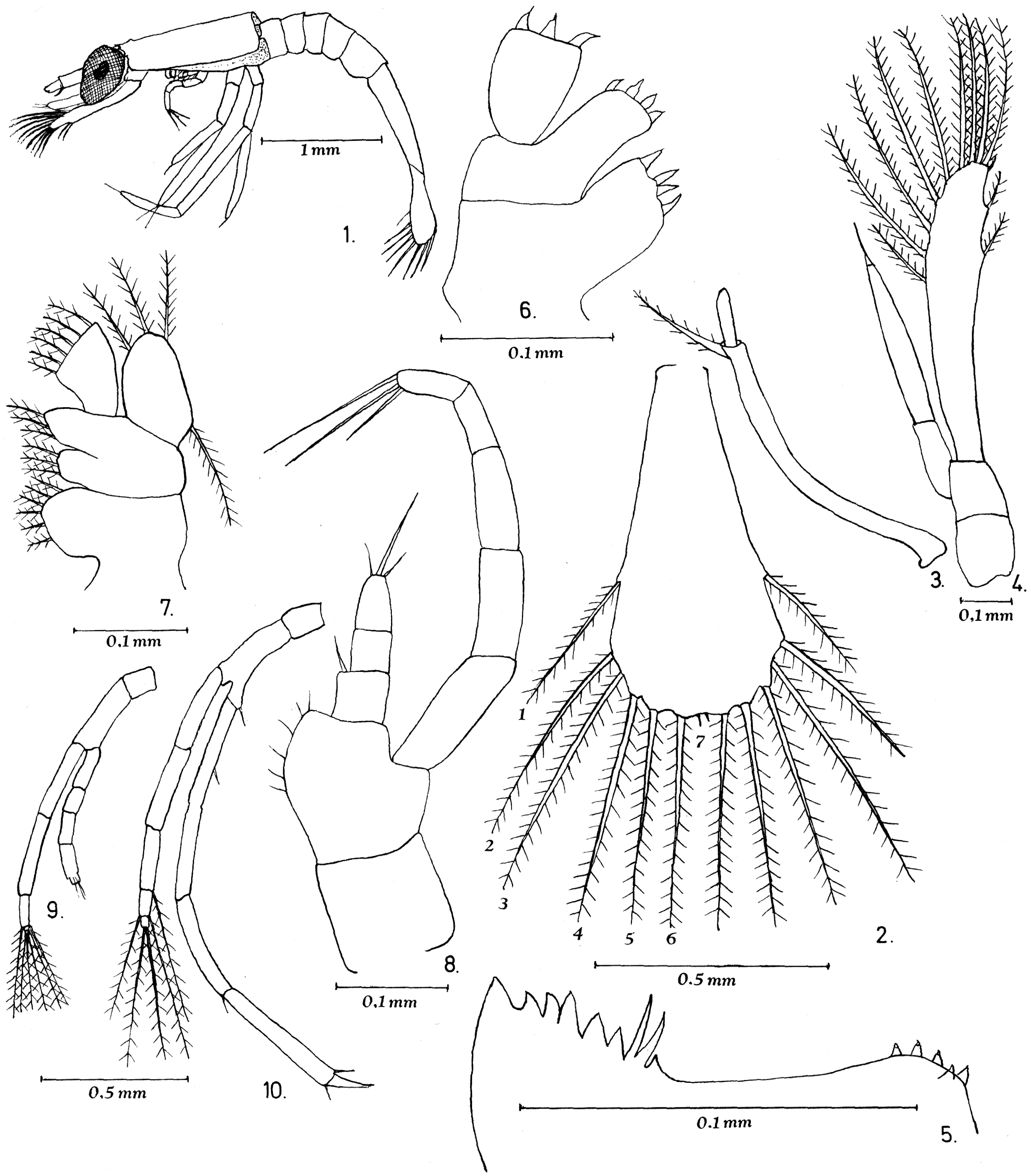


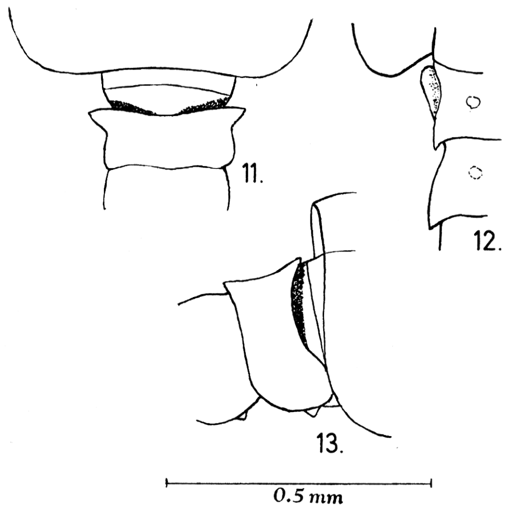
Figs. 1–10. *Amphion reynaudi*, Mysis I. Fig. 1, in total. — Fig. 2, telson plate. — Figs. 3–4, first and second antenna. — Fig. 5, cutting part of mandible. — Fig. 6, first maxilla. — Fig. 7, second maxilla. — Figs. 8–10, first to third maxillipedes.

Telson.

The telson is a spatula-shaped, ventrally hollowed plate with a rounded posterior border (Fig. 2) with two times seven spines of which the first six on each side are plumose; the medial pair, no. 7, is very small and plumose only from the second Mysis stage. The length of the spines increases from no. 1 to no. 3, nos. 3-6 being of about equal length. The setae on these spines are not fully developed and give the impression of being embryonic. This, together with the mouth appendages, stresses the point that this stage must be the first free larval stage, except that the hatching stage (often called the promysis stage) may remain for a very short time after hatching. As soon as the larva starts active swimming movements, however, the cuticle of the hatching stage is shed and the first freeliving stage, the first Mysis, appears. In 1966 I gave reasons for using the term Zoëa stage only for the brachyuran larva with its especially reduced characters, as was originally intended. For the non-Brachyuran and non-Penaeid larvae I use the terms Mysis stages.

Appendages.

The first antenna (Fig. 3) is two-jointed, The long basal joint ends in a strong, sabre-shaped, lateral spine with plumose setae. The second joint is very short and naked. The second antenna (Fig. 4) has a two-jointed protopod with about equally long joints. The exopodial antennal plate is widest in its distal part and nearly



Figs. 11–13. *Penaeus setiferus*, Mysis I, first abdominal segment with lateral process. Fig. 11, from dorsal. — Fig. 12, from ventral. — Fig. 13, from lateral.

three times the length of the protopod, reaching a little in front of the first antenna. It is furnished with 12 plumose setae: 2 shorter on the distolateral margin, one very short on the distolateral corner, three long terminally, and 6 along the distal third of the medial margin. The first joint of the endopod is about twice as long as wide, the second is very long, and in the following stage it begins to be annulated, the beginning flagellum. Already in this stage the endopod terminates in a seta.

The mandible is long, curved and without a palp. On its cutting edge (Fig. 5) is the beginning of both an incisor and a molar part. Starting laterally are about nine teeth in a line, then follows the whole middle part as a naked sharp-edged knife, and after that the molar part, on which some embryonic molar teeth are placed. A comparison with the following stages makes it apparent that the teeth originally are plumose setae which either shorten and lose their marginal hairs to become pointed, elongate incisor teeth or widen the rachis of the setae considerably to reach a conical shape which through losing of the hairs develops into a molar tooth (Figs. 26 and 26a). The shape and developmental stage of these teeth and especially of those on the following limb, the first maxilla, confirm that this stage must be the first freeliving stage. If the stage mentioned by Gurney (1942) is different from this, as previously discussed, Gurney's first stage must be a Promysis.

The first maxilla (Fig. 6) is three-jointed. Coxa and basale of the flattened protopod are each furnished with a medial lobe. The coxa is somewhat larger than the basale. The one-jointed endopod is of about the same size as the protopodial lobes. These lobes and the endopod are tipped with a few short and conical embryonic setae which not yet are plumose but are just setal buds which have broken through the surface. They are very much like the youngest setal buds on the mandible in the third Mysis stage (Fig. 26) which later develop as molar teeth. No exopod is present.

The second maxilla (Fig. 7) has also a two-jointed protopod, but only three medial lobes, the coxa has only one, the basale the normal two. All three lobes are provided with the usual plumose setae on their medio-distal margins, but these setae are relatively short and grow much longer in later stages. Both exopod and endopod are one-jointed and placed distally on the basale. The endopod is turned medially with its setae in line with those on the protopodial lobes. The exopod is turned forward and has no posterior lobe (HEEGAARD 1957). This is also the case for all known larvae of the Pandalidae, which also have only one medial lobe on the coxa (HEEGAARD 1957, Fig. 15).

The first maxillipede (Fig. 8) has two protopodial joints. The coxa is as wide as long, the basale is furnished with a hard, convex, medial edge in its distal half. This edge develops in the following stages into a lobe functioning as a masticatory process, but in this stage it is only a beginning swelling with a knife-sharp edge bearing a few short and soft hairs which a few stages later have grown into stiff, pumose setae on a toothed edge. The endopod has three about equally long joints. The first joint is provided with a medial keel and a distomedial seta. In the later development the keel will serve as a supplement to the masticatory process. The second joint is bare. The last joint is tipped with three setae of which the medial one is the longest. The exopod consists of five joints which diminish in both length and diameter proximo-distally. The first four joints are bare, the fifth is tipped with three very stiff setae. Judging from the placement of the exopod in relation to the mouth opening, it seems evident that it functions by carrying the prey to the mouth, holding it for the mandibles and cramming the food particles into the mouth.

The second and third maxillipedes are the locomotory organs. The second maxillipede (Fig. 9) has a two-jointed protopod with the distal joint nearly three times the length of the proximal. The exopod is three-jointed, the last and shortest joint is tipped with five or more stiff, plumose setae functioning as swimmerets. The endopod has four almost equally long joints, together a little shorter than the two first exopodial joints. The distal joint is tipped with two or more aesthetascs.

The third maxillipede (Fig. 10) is much larger than the second. The basale is longer than the coxa. The exopod is five-jointed, with the joints decreasing in length distally. The distal three joints are furnished with long plumose setae which form the swimming fan. The endopod is five-jointed, but the fifth joint is just a pointed claw in this early stage. The first three joints are of about equal length, no. 4 is a little longer. The endopod is nearly twice as long as the exopod and bears short, stiff setae and a terminal claw; this is rather unusual but makes it possible for the endopod to be the cleaning and trimming organ of the other limbs. The pereiopods have not yet begun to develop in this stage.

Dimensions.

Total length ca. 4 mm; length of carapace 1.2 mm; width of same 0.5 mm; rostrum 0.05 mm; abdomen 2 mm; telson 0.7 mm.

Mysis II

Figs. 14–22.

Development.

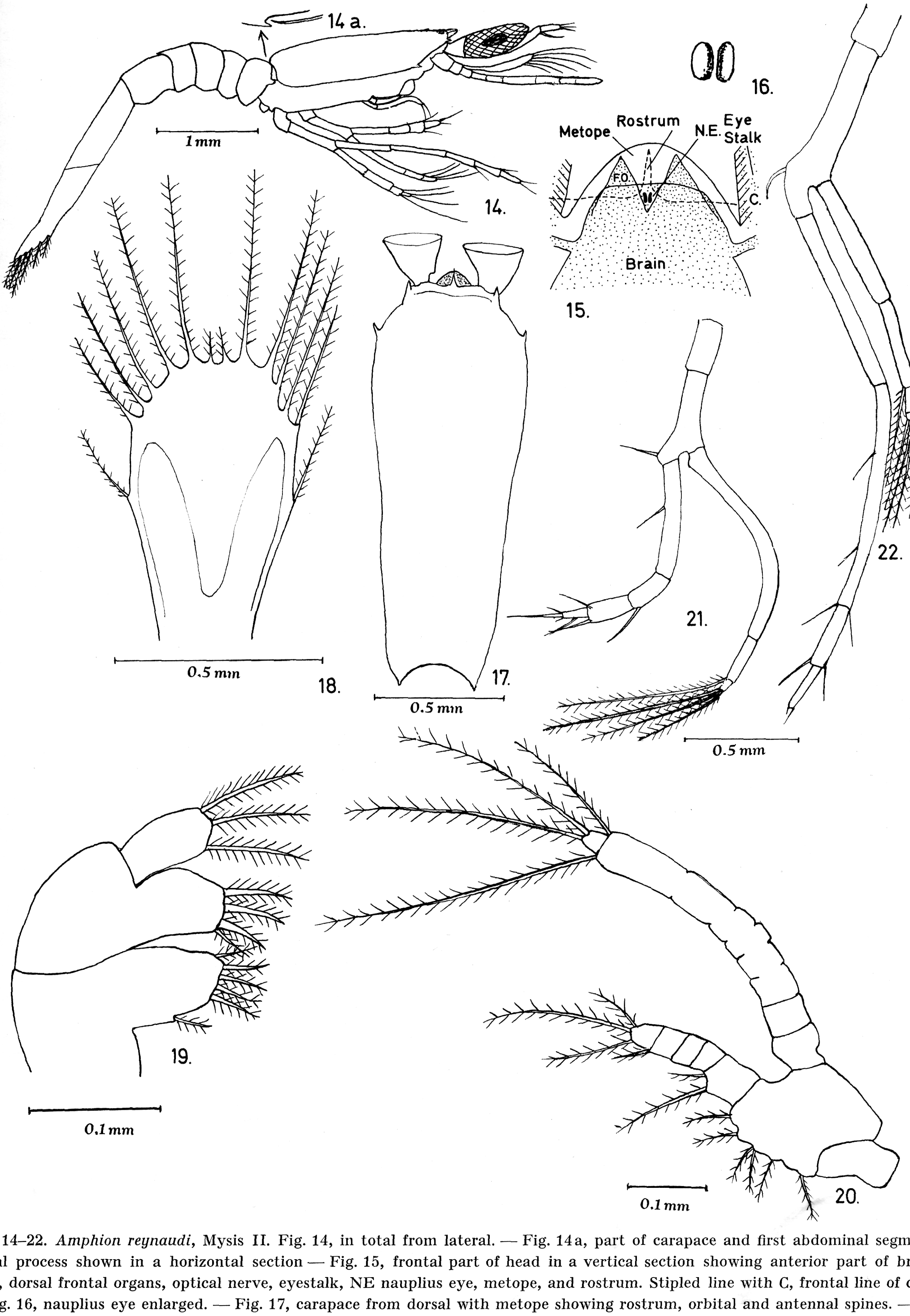
A little larger size; first antenna tipped with setae; beginning flagellum on the second antenna; setae developed on the first maxilla; coxa on first maxillipede reduced; five endopodial joints on second and third maxillipedes. First pereiopod a small bud; uropod visible either under the cuticle or as a pair of backwards directed buds placed ventrally on the telson. Seta no. 7 on telson plumose.

Thorax.

The thorax and with it the carapacc have grown considerably, the latter covering most of the thorax. The carapace (Fig. 17) has widened a little anteriorly and its posterior margin is no longer straight but distinctly concave. The rostrum reaches just beyond the metope, and both the orbital and antennal spines, as well as the cross ridge located on the anterior margin of the carapace, are more developed. Behind the ridge is the anterior dorsal organ.

Abdomen.

The abdomen is nearly unchanged in size. The lateral pleurae are a little better developed, as is the lateral process on the first segment, so that now the carapace can rest in the fold between the process and the segment (Fig. 14a).



Figs. 14–22. *Amphion reynaudi*, Mysis II. Fig. 14, in total from lateral. — Fig. 14a, part of carapace and first abdominal segment with lateral process shown in a horizontal section — Fig. 15, frontal part of head in a vertical section showing anterior part of brain with F. O., dorsal frontal organs, optical nerve, eyestalk, NE nauplius eye, metope, and rostrum. Stipled line with C, frontal line of carapace. — Fig. 16, nauplius eye enlarged. — Fig. 17, carapace from dorsal with metope showing rostrum, orbital and antennal spines. — Fig. 18, telson from ventral with uropod buds under the cuticle. — Fig. 19, first maxilla. — Figs. 20–22, first to third maxillipedes.

Telson.

The telson is wider, with a more rounded posterior margin and thus is more spoon-shaped ventrally. In the second Mysis stage setae no. 7, the small pair in the medial line, have enlarged a little and become plumose.

Appendages.

The first antenna, which had a bare tip in Mysis I, is now tipped with three short setae. It has grown a little and the dorsolateral concavity following the curve of the eye is still present; later it disappears. The second antenna has an enlarged protopod. The flagellum tipping the single endopodial joint has started to develop and consists of six to eight rings. The exopodial antennal plate has become more rounded and its marginal plumose setae are more forming a fan, but no antennal spine has yet developed.

The labrum is a semicircular, hollow plate with a small incision medially on the posterior margin.

The mandibles have now both soft and stiff setae on the cutting edge. The setae are of pyramidal shape on the molar part, thereafter both stiff and flexible ones on the edge between the molar and incisor part, and finally, the 7-8 incisor teeth have been pressed together to enlarge the now hairy edge between molar and incisor teeth. This development continues in the following stage (Fig. 26), where it shall be further considered.

The labium is furnished with two squarish lobes placed far apart and both seem to be naked in this early stage.

First maxilla (Fig. 19). The few embryonic setal buds on the endites or masticatory medial processes and on the endopod have now developed into the same number of plumose setae: 3 on the endopod and 4 on the basale endite. Only on the coxa endite has the number increased, from four to six, including that for a first maxilla characteristic most proximal seta usually placed a little apart. This setal development is interesting firstly, because it supports the point of view that this Mysis I must be the first free-living stage, and secondly because it follows the same sequence as the development of the molar and incisor teeth on the mandible, perhaps with the exception of a few primary incisor teeth. This seems to show that the teeth of the mandible are developed from transformed plumose setae. The first maxilla is without an exopod.

The second maxilla has grown a little and has lost its last embryonic characters. Its setae are longer and more numerous; on the anterior margin of the exopod are four setae and on its lateroposterior corner two, of which the most anterior is short and points forward.

First maxillipede (Fig. 20). The coxa has become reduced and is from now on only a short stalk linking the limb to the cephalothorax. The convex medial cutting edge of the basale has developed from a smooth to a toothed margin with plumose setae between the teeth. These setae were in the first Mysis only thin hairs (Fig. 8). They number six in both stages. The endopod is now five-jointed through a division into two of the original second and third joints, not because of adding joints at the tip. Thus the first joint remains unchanged, but it has developed a second seta and a larger medial, edged process. The fourth joint has disto-medially a small seta, and the distal joint has three terminal setae. All the setae are plumose. The exopod has elongated but has lost its distinct five joints and is now divided into eight to ten indistinct joints which give it an improved flexibility. Only the two proximal joints and the most distal one are clearly delimited. Each of the two last joints has two long and stiff setae which function in the feeding mechanism, first by clasping and holding the prey to the grinding stones of the mouth appendages and later by pressing the food into the mouth.

The second and third maxillipedes (Figs. 21 and 22) develop into locomotory organs with long exopodial swimming fans. As in the previous stage the third maxillipede is larger than the second. In later larval stages the second and the third maxillipedes can only be distinguished from the thoracopods by their position and enervation. Therefore, it could be justified to claim that *Amphion* has only one pair of maxillipedes, the first pair, and that the rest of the thoracic limbs are pereiopods. This would be a more primitive character than found in other decapods, but against it speak (1) that the larva hatches with all three pairs of maxillipedes functional, but with none of the following pereiopods, and (2) the placement, enervation and later gill provision of the two last maxillipedes.

In the second maxillipede the basale is only twice as long as the coxa. The endopod is now five-jointed through the addition of two small joints at the tip. Further, the limb has developed setae: medially one seta on the basale and on the endopodial joints 1, 3 and 4, one laterally on nos. 2 and 3, two on no. 4, finally a long distal seta on no. 5. The exopod is still three-jointed but its basal joint is now longer, being four times the length of the following joint. The third and distal joint is the shortest. The whole exopod is only a little longer than the endopod of the same limb. In the third maxillipede and in all fully grown pereiopods of the later stages the exopod is much shorter than the endopod. As the *Amphion* larva lives in the upper 50 meters of the oceans these well-developed endopods cannot function as walking limbs, and lacking any swimmerets they can have no function as actual locomotory organs, but seem to function as a food trap for smaller organisms.

The third maxillipede (Fig. 22), which is the largest limb on the larva, is built entirely as a pereiopod. The basale is further extended in length compared with the second maxillipede or with the previous stage. The basale has four to five times the length of coxa. The endopod is long, four-jointed, and its most distal joint, the claw in the previous stage, has grown into a full joint. The setae developed on the medial side are 1 on basale and on the endopod joints medially 0, 3, 1, 1, laterally 0, 1, 1, 1. The exopod is unchanged and therefore comparatively shortened.

The first thoracopod or pereiopod is present as a tiny bud behind the maxillipedes.

No pleopods are present.

Dimensions.

Total length 5.5 mm; length of carapace 1.8 mm; width of same 0.6 mm; rostrum 0.08 mm; abdomen 2.2 mm; telson 1 mm.

Mysis III

Figs. 23–27.

Development.

Larger; rostrum reaches beyond the metope (Fig. 23); the telson is more elliptical and has lost setae nos. 1 and 2. The flagellum of the second antenna has enlarged by division and subsequent growth of joints. The mandible is more setose. The first pereiopod is visible with a short unjointed protopod, elliptical, unjointed exopod and endopod. The uropod has developed and consists of a large exopod with plumose setae and a small embryonic endopod with embryonic setae.

Thorax.

The thorax has grown more than the carapace, which does not cover the posterior part of the thorax. The posterior part of the carapace has started to flatten out to overreach the edges of the body as is characteristic for older *Amphion* larvae. Both the orbital and antennal spines have enlarged, and the tip of the rostrum now reaches beyond the metope.

Abdomen.

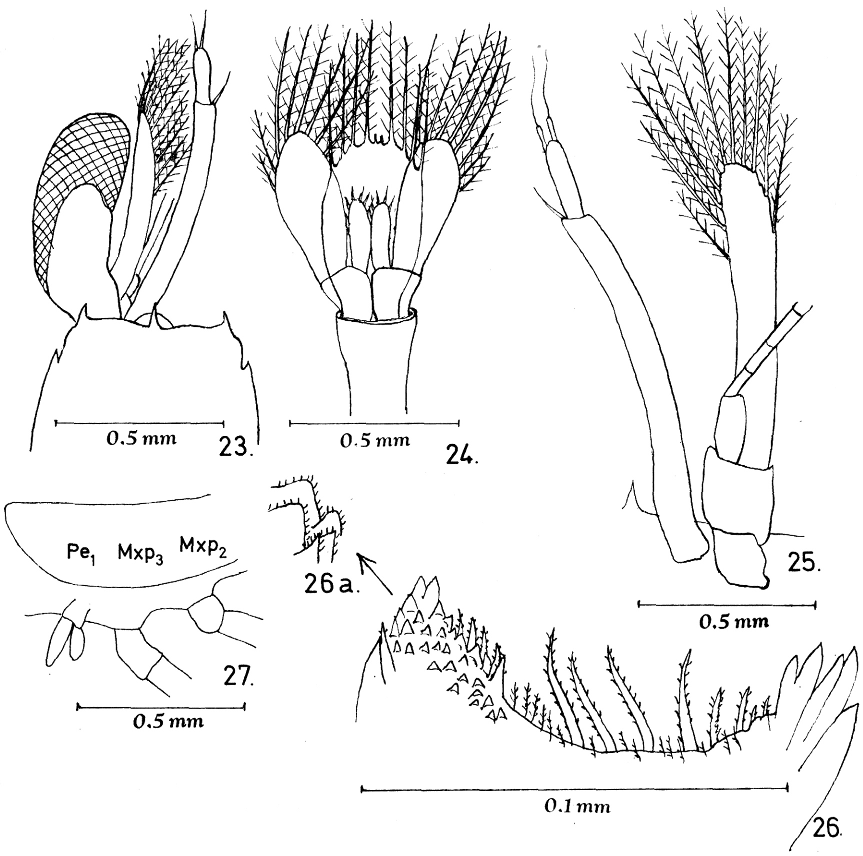
No larger changes have taken place in the abdomen which now is only a little longer than the thorax. The lateral process on the first abdominal segment has become a little more pointed.

Telson.

The telson has changed (Fig. 24). In the two first Mysis stages its base was more cylindrical towards the last abdominal segment and appeared as a prolongation of this segment. But after the development of the uropods this part of the telson has flattened to give room for the uropods, and its proximal part has widened so that the whole telson now is shaped as an elliptical plate with the setae extending only from the distal fifth of its length, this due also to the loss of setae nos. 1 and 2, with only four long, plumose setae and two very short ones remaining (Fig. 24). The shape of the telson changes so much through each larval stage that it provides the easiest character for numbering the stage of a larva at a first examination. The telson plate is twice as long as its largest width.

Appendages.

The first antenna (Fig. 25 left) is nearly unchanged with a long basal and a short distal joint; the latter later develops into the lateral flagellum of the first antenna. It is in this stage tipped with two aesthetascs. The basal joint is most laterally tipped with the curved, plumose spine present in all stages. The second



Figs. 23–27. *Amphion reynaudi*, Mysis III. Fig. 23, frontal part of carapace from dorsal and metope, first and second antenna, and eye. — Fig. 24, sixth abdominal segment from ventral with uropods and telson plate. — Fig. 25, frontal part of carapace from ventral with first and second antenna, metope excluded. — Fig. 26, incisor and molar edge of mandible. — Fig. 26a, enlargement of some molar teeth. — Fig. 27, posterior part of thorax from lateral.

antenna (Fig. 25 right) has still a two-jointed protopod. The exopodial antennal plate is more elongate, but the number of setae along its margin is still eleven. Of these setae the one placed most lateroposteriorly on the margin will later develop into the antennal spine or hook. The endopod is one-jointed and tipped with a ringed flagellum. Its length cannot be determined because it is broken in the whole material. Only in a single larva of the next stage, Mysis IV, was the right flagellum intact, with 12 rings.

The mandible (Fig. 26) shows an interesting development. The original incisor teeth have been pressed together and cover now less than one fifth, against earlier one third of the cutting edge. The number of molar teeth has increased considerably and they more or less cover the dome of the molar part. They are not yet developed as proper molar teeth but only as conical protuberances which at a closer examination (Fig. 26a) appear as flattened, pyramidal-shaped, plumose setae. Later the plumose part of the seta disappears and the grinding cone of a molar tooth is left. On the sharp edge between the incisor and molar teeth, longer and shorter hairs have grown out. They appear still as soft and flexible and are embryonically plumose. The smaller ones will later either disappear or grow to the full size, lose the plumose covering, develop a massive cuticle and in this way be transformed into the characteristic styliform incisor teeth placed on the ridge between the primary incisor and molar teeth on the mandible of older larvae and on the mandible of many other Crustacea, especially decapods. No palp exists in any of the known larval stages of *Amphion*.

The first and second maxillae are in general unchanged from the previous stage. Only the endopod on the first maxilla has decreased a little in size compared with the other parts of the limb and has started the first part of its 90° turn from a transverse to a longitudinal axis, with the distal setae pointing medially to a longitudinal axis in prolongation of the stem. (For explanation compare Figs. 19 and 38.)

In the first maxillipede the medial ridge on the coxa has enlarged a little and developed a few more setae. The second and third maxillipedes are unchanged, but the first pereiopod has started to develop (Fig. 27), although it is still nonfunctional and very short. Its protopod is unjointed and about as long as wide. Exopod and endopod are present, but only as small elliptical leaves on the protopod.

No pleopods are visible, but the uropod has developed. In the second Mysis the uropod was a backwards pointing stick either visible under the cuticle or free of the cuticle. Now (Fig. 27) it has developed a one-jointed, almost squarish protopod, with a large leaf-shaped exopod, which extends to the tip of the telson and is furnished with 7–8 plumose setae as long and as well-developed as the setae of the telson, except for the two most lateral ones. The protopod and exopod are functional. The endopod is short and non-functional, only half as long as the exopod; it is an elliptical, flattened leaf, lined with short and still embryonic setae.

Dimensions.

Total length 5.8 mm; length of carapace 2 mm; width of same 0.7 mm; rostrum 0.09 mm; abdomen 2.6 mm; telson 0.8 mm.

Mysis IV

Figs. 28–32.

Development.

The largest changes are in size and in the shape of the telson. The antennal keel and the cervical groove on the carapace are more dominant than in the previous stage.

No special changes have taken place in the abdomen, but the telson has changed into a flattened plate with nearly parallel sides and with setae nos. 1–3 lost or nearly lost; there may be a small vestige of the third seta on one of the sides. Further, seta no. 4 has shortened to only half the length of the two following. The first and only flagellal joint on the first antenna is more elongate, and the flagellum of the second antenna is 12-jointed and furnished with aesthetascs and sensory hairs on the distal two thirds of the margin of each joint.

The first pereiopod has only developed a little further.

Thorax.

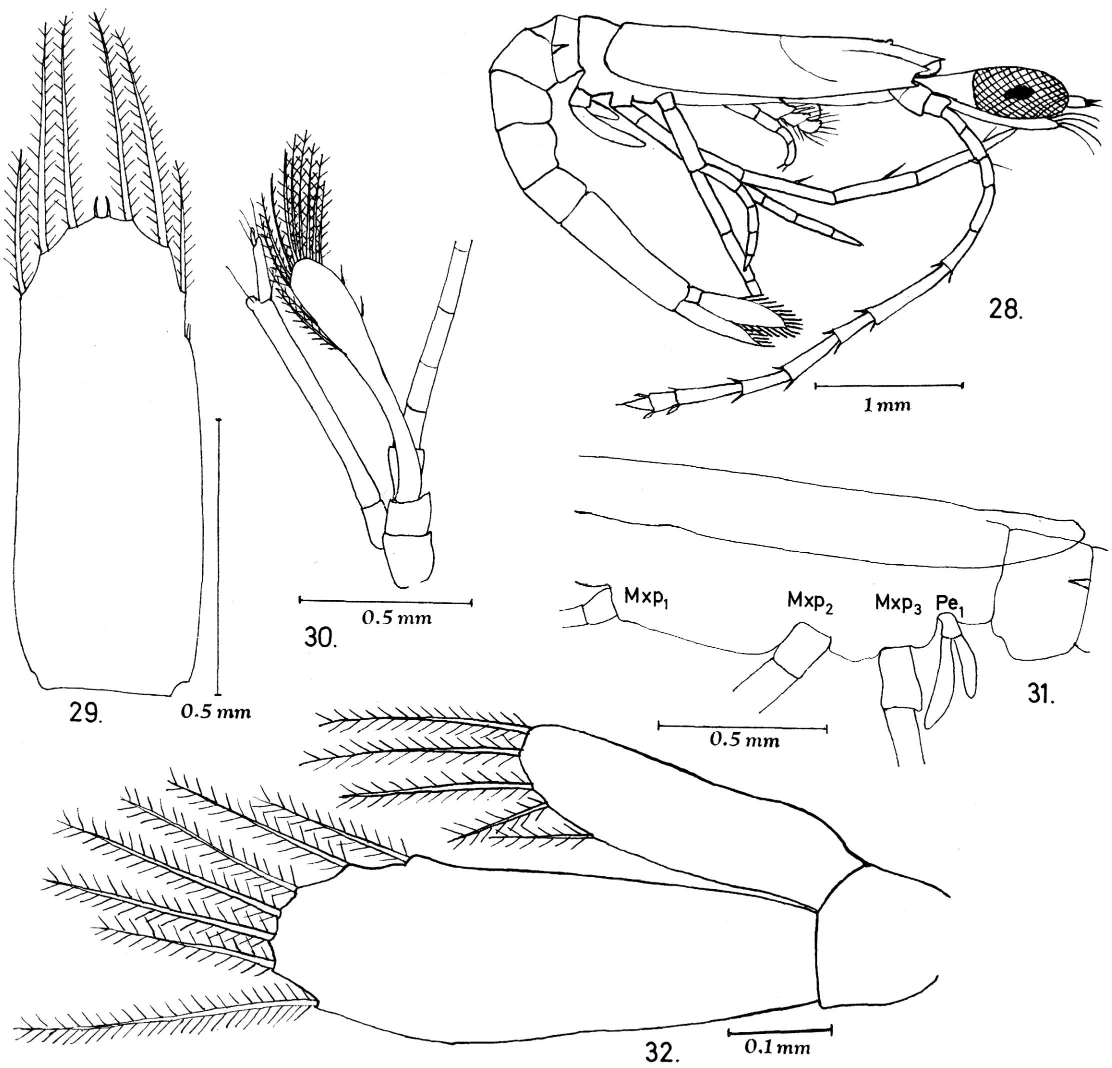
The carapace seems a little more flattened and has developed a keel running backwards from the orbital spine for about two thirds of the distance to the cervical groove, this latter being now more pronounced (Fig. 28).

Abdomen.

No changes were observed.

Telson.

The telson (Fig. 29) is no longer tube-shaped towards the sixth abdominal segment, but is right from its base a flattened horizontal plate extending from the dorso-posterior margin of the sixth abdominal segment, with the base of the protopod of the uropods filling the ventral half of the margin. The elliptical outline of the telson plate is lost, and it has nearly parallel margins from its base to the beginning of the setae. The



Figs. 28–32. *Amphion reynaudi*, Mysis IV. Fig. 28, in total from lateral. — Fig. 29, telson plate. — Fig. 30, right first and second antenna. — Fig. 31, posterior part of thorax and first abdominal segment. — Fig. 32, uropod.

number of setae is further reduced with only nos. 4–7 left, and no. 4 is only half as long as the two following. Sometimes a small vestige of seta no. 3 is left on one of the sides. Finally, the telson plate has grown from about 0.5 mm to 0.8 mm in length.

Appendages.

The appendages have not changed much. This makes the stage a little doubtful.

The flagellar joints of the first antenna are a little more elongate. The laterodistal spine on the first joint of the antenna, which in all previous stages was strong and sabre-shaped, is lost and replaced by a normal seta. One specimen had a 12-jointed flagellum on the second antenna, extending from the unjointed endopod (Fig. 28). The distal joints in the flagellum are the longest except for the two last, not fully grown ones. The first joints are bare, and each of the following 7 joints has distally two sensory setae placed opposite to one another. The last joint is tipped with one small seta. On the exopodial scale the two most lateral setae are reduced, but no antennal spine is yet present. In the mandible the hairs on the ridge — the future secondary teeth — have become a little more plumose and the molar teeth in the cone a little larger and more compact. On the first maxilla the endopod is turned a little more towards the longitudinal axis of the appendages. The maxillipedes are slightly stouter, and the first pereiopod is a little larger, especially its two branches, but no more joints have been added.