Table I. *Amphion reynaudi.* Dimensions in mm.

Mysis stage no.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Total length . .	4	5.5	5.8	6	6.5	7	8	9	9.5	13	17	23	25
Carapace	1.2–0.5	1.8–0.6	2–0.7	2.2–0.8	2.7–1	2.8–1.2	3.5–1.5	4.5–1.6	5–1.6	7–2	8–3	13–4	14–4.5
Rostrum	0.05	0.08	0.09	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.3	0.3	0.3
Abdomen	2	2.2	2.6	2.6	2.6	3	3.2	3.2	3.2	4	6	8	9
Telson	0.7	0.8	0.8	0.8	0.8	1	1.1	1.2	1.2	2	2.5	2.5	2.5
Growth-factor		1.38	1.05	1.04	1.08	1.07	1.14	1.13	1.05	1.38	1.31	1.35	1.08

Postlarva I

Figs. 117–129, 136.

Localities.

Dana St. 4003 IX, 8°26′ S, 15°11′ W. 4000 m wire, S. 150, 120 min., 9.3.1930, 11 a. m., 1 specimen.

A single specimen of this stage was found in the "Dana" material from the South Atlantic together with 3 specimens of the following stage and 1 adult ("*Amphionides*").

This and the following stages are not true postlarval stages, but transitional forms to the abyssal stage and could therefore also be called Amphionides stages 1, 2 and possibly 3, but for the sake of convenience the term Postlarva has been used in this paper.

Development.

This is a most interesting intermediate form to "*Amphionides valdiviae*", also as it was found in a haul with 4000 m wire, which means nearly 2000 m below the surface. The carapace has started to inflate and a rostral plate has developed, with the rostrum pushed forward at its tip. Both orbital and antennal spines are lost and in their place the carapace has started to develop lobes. Although the specimen was much damaged, it still could be seen how the first maxilla, the endites and the endopod of the second maxilla, and the large masticatory endite of the first maxillipede were strongly reduced. The following maxillipedes and all the thoracopods were still present, also the fifth thoracopod, but much reduced. The pleopods have developed further, and even the first pleopod has begun to develop an appendix interna on the endopod. Lateral process on first abdominal segment still present.

Thorax.

Because the single specimen in the collection was much damaged no complete description of the carapace can be given. The carapace, of which only the anterior part was present (Fig. 117), has enlarged. In front a lobate rostral plate has developed like a pointed bulb between the first antennae and with the small rostrum at its anterior tip. The metope is placed ventroposterior to the rostral plate. Both orbital spine and antennal spine are lost although these spines have steadily enlarged from stage to stage up to the last Mysis stage. In the place of these spines small forward-pointing lobes have started to grow, so that the front of the carapace now shows a convoluted line with five lobes, the rostrum pointing out from the middle one. Also some lumps of the posterior part of the carapace were present, showing that the transformation of the carapace into the tissue-paper-like substance described by Gurney (1936) for *Amphionides valdiviae* has started. At the same time the carapace has started to enlarge, especially laterally.

Abdomen.

The abdomen has enlarged from the previous stage, especially its appendages. The lateral process on the first abdominal segment which keeps the carapace from sliding backwards is still present. The cuticle on the abdomen gives the impression of being thinner than in the surface forms, a difference which develops further in the later stages.

Telson.

The telson is long and pointed posteriorly, and the vestige of the sixth pair of setae is lost and replaced by a pair of tiny, thin hairs.

Appendages.

A strong reduction has taken place from the previous stage. This is best seen by comparing BATE's figure from his Challenger Report (1888) of the oldest *Amphion* larva (Pl. 148) with the figures in the present paper (Figs. 117–129) of the following stage, the first transitional stage to the abyssal life in 2000–4000 m depth.

The first antenna has not changed much except that the two flagella seem to be well developed. They are both broken a little from their base, but what is left is divided into many short joints as in adult decapods. Further, the lateral flagellum is much thicker than the medial one. The preservation is poor and olfactory hairs or other sense organs could not be seen, but they are possibly already present, presumably on the missing distal part of the flagellum.

The second antenna has also developed with the endopod as a long many-jointed flagellum, but also this is broken near its base, as shown on Fig. 117. The main and interesting change has taken place in the exopodial antennal plate. In the preceding surface stage the antennal plate was lancet-shaped with a long spatular handle (Fig. 100). In the Postlarva III the antennal scale (Fig. 143) is nearly quadratic, without stalk or handle, and with the plate reaching straight to the base. In this first transitional stage the plate has widened considerably into a more elliptical plate which, though most narrow at the base, has lost the handle. This, together with the antennal plate and other characters of the following stage, shows a natural developmental line from *Amphion* towards "*Amphionides*".

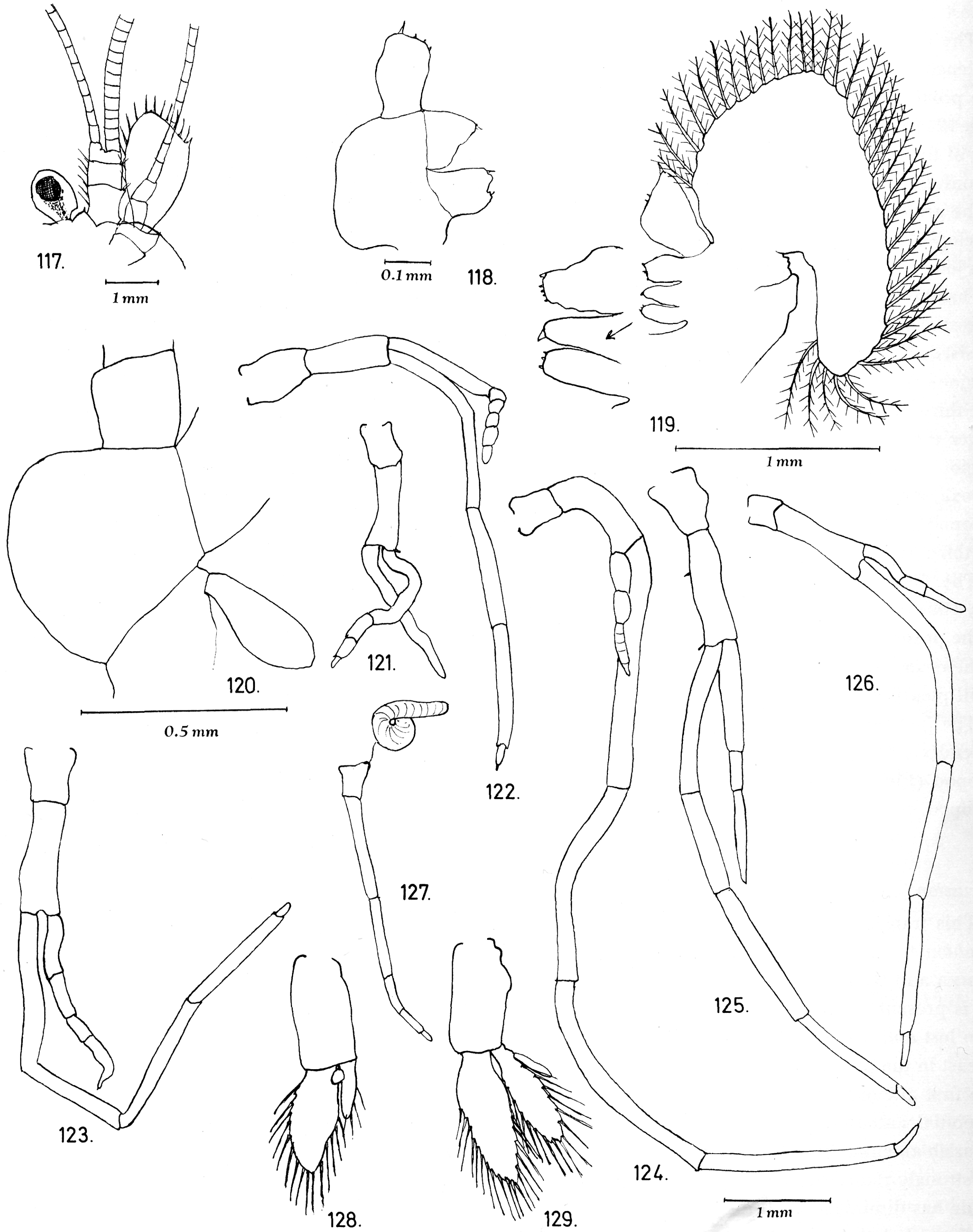
Due to the very poor state of preservation of the single larva of this stage in the material, the maxilla and and part of the first maxillipede were the only mouth appendages present.

The first maxilla (Fig. 118) is strongly reduced from a wellfitted organ for brushing, holding and tearing the food to a nonfunctional vestige which in the following stage practically will have disappeared. The two masticatory endites are reduced and their setae are tiny and vestigial without any function. Also the endopod is strongly reduced. In the preceding surface stage the endopod (Fig. 107) functioned as a third masticatory endite with a weak division into two joints; now it is only a small, unjointed lump on the protopod with three to four tiny spines at the tip, vestiges of the former strong and stiff setae.

Also the second maxilla (Fig. 119) has started its transformation to fit the new way of life. The three masticatory endites on the protopod are still present, but they are reduced and have lost their setae; also here only small vestigial spines remain of the former setae. A reduction has also taken place in the endopod, and its square-cut distal margin is transformed into a more pointed tip. At the same time the endopod has started a rotation back to its original longitudinal axis, which was given up around the fifth Mysis stage to let the endopod function as a masticatory process together with the endites of the protopod. Finally, the anterior part of the exopod has grown and widened from about $^1/_2$ of the exopod to about $^2/_3$ of it.

In the first maxillipede (Fig. 120) the basale and the first endopodial joint in the last surface stage (Fig. 109) were shaped as masticatory processes, of which that on the basale was very large. This latter has been much diminished, and the process on the first endopodial joint has practically disappeared. The rest of both the endopod and exopod was missing in the specimen at hand.

The following two maxillipedes and all the pereiopods, except the second, are strongly reduced without setae or well-developed spines, and appear to be completely unfunctional. The second maxillipede (Fig. 121) has a two-jointed protopod with the second joint most reduced — to only twice the length of the first joint. The exopod is reduced to an unjointed, thread-like organ of the same length as the protopod. The endopod, which is about as long, has remained four-jointed, but the whole limb is delicate, absolutely nonfunctional, and without a gill at its base. A tiny vestige of the spine on the basale at the base of the endopod was present. The third maxillipede (Fig. 122) has also shortened, but less than the second. In the protopod the second joint is only a little longer than the first joint, the exopod has the first joint well developed although shorter



Figs. 117–129. *Amphion reynaudi*, Postlarva I. Fig. 117, anterior part from dorsal showing rostral plate and beginning of orbital and antennal lobes. Further, first and second antenna and the eye in beginning transformation. — Figs. 118–119, first and second maxilla. — Fig. 120, proximal part of first maxillipede showing coxa and basale, mastigobranchia and proximal parts of exopod and endopod. — Figs. 121–122, second and third maxillipede. — Figs. 123–127, first to fifth pereiopod. — Figs. 128–129, first and second pleopod.

than in the previous stage and the five following small joints are so delicate that they look as if they could be lost any moment. The limb has a phyllobranchia at its base.

The first pereiopod (Fig. 123) is only slightly longer than the last maxillipede. The basale is about twice the length of the coxa. The exopod is four-jointed but delicate and without setae. The endopod is four-jointed. The proximal joint is the longest and the most distal joint is very short and bud-like. The second pereiopod (Fig. 124) is in a peculiar transitional stage, its protopod is shorter and thinner, but its cuticle is firm and that of the endopod is with muscles inside, while such muscles are decaying in the other limbs. The exopod is nonfunctional and reduced to an appendix with two larger joints at the base and five smaller ones distally. In the protopod the second joint is two and a half times the length of the first joint, and the endopod has now developed a fifth joint. The four proximal joints are long and slender and of about equal length, and the distal fifth joint is like a small claw at the tip of the endopod. The endopod seems by this to be unchanged in length but has lost all its spines. A pleurobranchia is found at its base. The third pereiopod (Fig. 125) is the second longest of the limbs. The basale is twice as long as the coxa and vestiges of its two spines remain. The exopod consists of three joints, of which the medial is the shortest. The endopod is five-jointed in contrast to the previous stage with a four-jointed endopod. Peculiarly enough, the fifth joint is developed both in the second and third pereiopods. The endopodial joints are long, the first and third a little longer, the fourth slightly longer than the second, the fifth very short. Also here a pleurobranchia is placed at the base. The fourth pereiopod (Fig. 126) is still a little shorter and not so stout as the third. The basale is three times the length of coxa, which is very short compared with the coxa of the third pereiopod. The exopod is three-jointed. The endopod is four-jointed with three long joints and a short joint at the tip. A gill is found at the base of both the third and fourth pereiopods.

The fifth pereiopod (Fig. 127) is present. In the previous stage, the last surface stage, this limb (Figs. 116, 102) had a protopod and an exopod, but no endopod and no setae, and only two spines on the basale. In the present stage the parts remain with a two-jointed protopod of which the basale is three times the length of the coxa, after which follow four exopodial joints. The gill-bud from the previous stage has developed into a full pleurobranchia and so has the gill of the fourth pereiopod; all other gills are about unchanged.

The pleopods have developed further. They are all with setae both on exopod and endopod. Further the appendix interna (Fig. 129) is now fully delimited from the endopod. Of special interest is that the first pleopod (Fig. 128), which is the last of the pleopods to develop, has developed setae on both exopod and endopod as well as a small appendix interna on the endopod.

Discussion.

This transitional stage is of the greatest interest for the understanding of the further transformations of *Amphion* to fit its abyssal habitat. Moreover, it explains the mentioning of a female in "*Amphionides*" by Zimmer and Gurney. The stage has developed a rostral plate which did not exist in the "last" *Amphion* stage but is present in "*Amphionides*"; the rostrum is placed at its tip, the orbital spine and antennal spines have been lost and are replaced by lobes from the carapace. The tissues of the carapace have become paper-like, at least in the preserved material, as in "*Amphionides*", but the setae along its margin have not yet developed. The first antenna and the endopod of the second antenna have developed long, many-jointed flagella. The exopodial antennal plate has lost its elongate form with a handle and become elliptical, approaching the squarish antennal plate of "*Amphionides*". The first maxilla and the endites and endopod of the second maxilla are strongly reduced, but the anterior lobe of the exopod has widened, while the gnathobase on the first maxillipede has diminished. All these characters point from *Amphion* towards "*Amphionides*". The following limbs on the cephalothorax are the same in number, but strongly reduced from the previous stage. Of special interest is the fifth pereiopod which appeared in the previous stage together with its gill-bud; in this stage the limb is reduced, but its gill-bud has developed into a proper gill which is the more interesting as both gill and limb disappear totally in the following stage. Further, the fact that the first pleopod in this stage has developed an appendix interna and therefore now is in line with the development of the other pleopods stresses the view (see p. 34) that the pleopods in *Amphion* develop from the last to the first pair. From the tenth Mysis to this 14th larval stage of *Amphion* we have now an unbroken developmental line for the pleopods which, together with the presence of the fifth pereiopod, contradicts all previously published explanations of sexual characters in the appendages.

Further, ZIMMER (1904, p. 227–28) writes about the "female" of "*Amphionides*" the following: "Die Antennenschuppe ist etwas schmäler zur Länge als beim Männchen. Der Exopodit des 2.–7. Cormopodenpaares ist lang, jedoch ungegliedert. Das 8. Paar ist vorhanden, trägt aber keinen Exopoditen. Das 2. bis 7. Paar ist 7-gliedrig, das 8. Paar 6-gliedrig. Kiemen sind am 3. bis 8. Paar vorhanden. Die Pleopoden sind mit Ausnahme des ersten wie des Männchens gebaut. Der erste gleicht den andern nur dass er einästig ist."

This description differs in minor points — the joints of the first antenna and the thoracopods — from the here-described *Amphion* stage. For the fifth thoracopod ZIMMER calls the exopod an endopod, a mistake arising from his not realising its relation to the same limb in the last *Amphion* stage. Further, for the one-branched first pleopod there may be two explanations. The first is that ZIMMER overlooked the small endopod, as his description is only a preliminary one and incorrect in many other details — his numbers of joints in the appendages do not always agree with the present investigation, but the limbs are very delicate, and it is easy to overlook a joint, however, my description corresponds with the jointing of *Amphion*. The second explanation may be that ZIMMER is partly confusing this and the following stage because there the first pleopod is also unbranched in the latter, but here the fifth pereiopod is missing, as ZIMMER mentions in his description of the *Amphionides* female.

GURNEY (1936, p. 398) only refers to ZIMMER's description of a female *Amphionides*, but in 1942 (p. 225) he writes: "In other specimens, which are assumed to be female, the legs are rather less reduced, the fifth leg being present, and pleopod 1 differs from the succeeding pairs only in the small size of the endopod." This is for the first pleopod in disagreement with ZIMMER, but agrees in all details with the description of the above-described Postlarva I of *Amphion*.

I feel that this, together with what has been discussed under *Amphion* concerning sexual characters in existing gonads and differences in the appendages of the larvae, clearly shows all these characters to be only stages in a normal developmental line and not — as discussed in the existing literature — sexual dimorphism. Therefore no discussions of sexual dimorphism can be supported by the material of *Amphion* and "*Amphionides*" which is known up to the present.

Postlarva II

Figs. 130–135, 137.

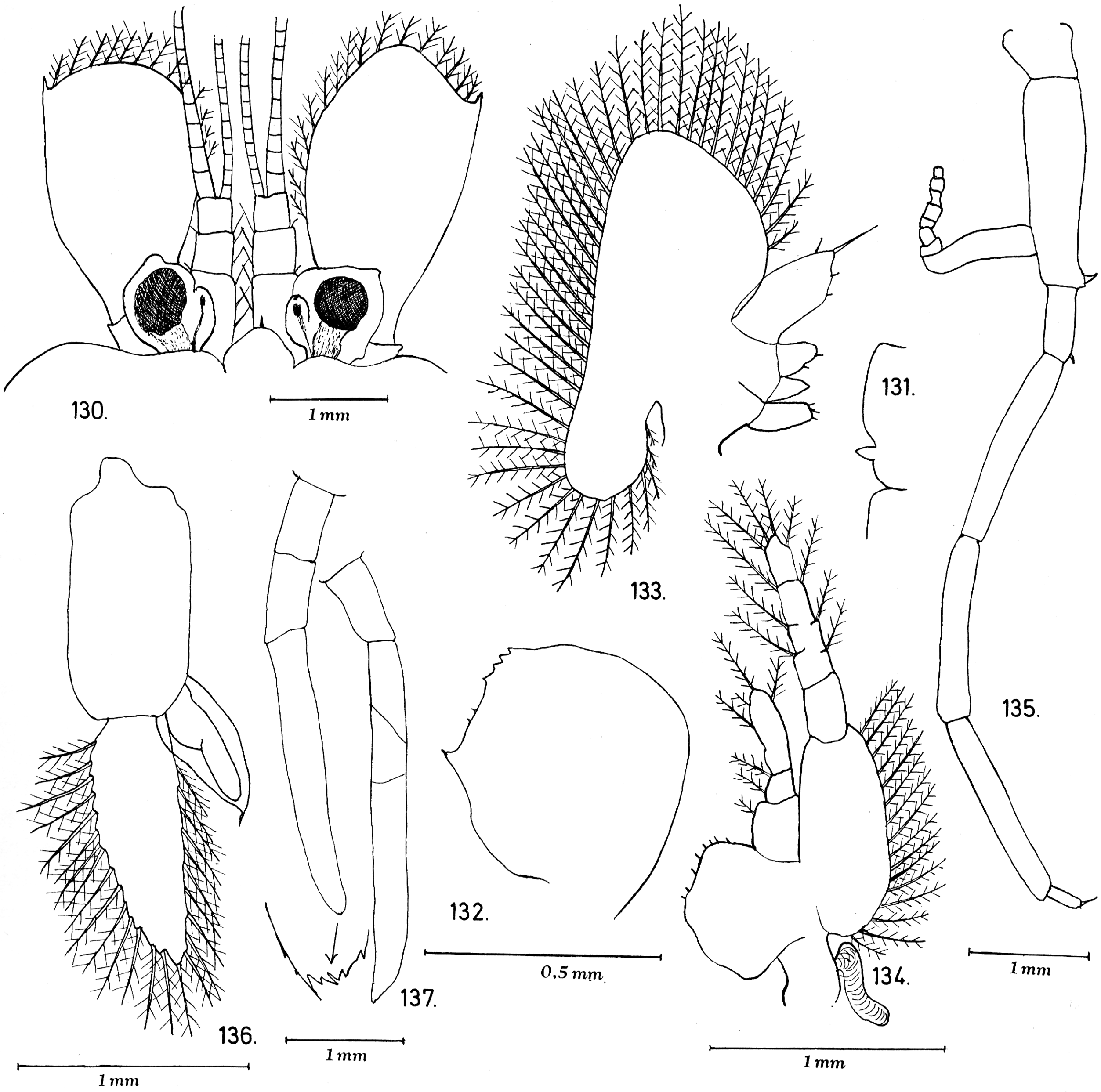
Localities.

"Dana" St. 4003 IV, 8°26′ S, 15°11′ W. 3000 m wire, S. 150, 120 min. 9.3.1930, 11 a. m. 3 specimens.

Three specimens were found, together with the one specimen of Postlarva I, on "Dana" St. 4003 IV, 3000 m wire, in the South Atlantic.

Development.

The whole carapace, the rostral plate, and the orbital and antennal lobes have enlarged. The antennal plate of the second antenna has widened. The luminescent organ in the eye has started to develop. The mandible has shortened and is almost without teeth, the first maxilla is reduced to a small lobe with a few hairy setae at the side of the mouth. In the second maxilla the endites have further shortened and the endopod has decreased a little. The maxillipedes and pereiopods, except the first, are reduced further, especially their exopods, and only the second pereiopod is larger, while the fifth pereiopod has disappeared entirely, together with its gill. The rest of the gills are unchanged. The first pleopod has lost its setae and endopod, the rest has grown in length, now forming a rod. The following pleopods and especially their setae have enlarged. The telson is pointed with a pair of short, hairy setae at the tip.



Figs. 130–137. *Amphion reynaudi*, Postlarva II. Fig. 130, anterior part of carapace from dorsal showing rostral plate and rostrum, orbital and antennal lobe, first and second antenna, and the further transformation of the eye with the beginning development of the luminescent organ in the eye. — Fig. 131, first abdominal segment with the lateral process. — Fig. 132, mandible. — Fig. 133, second maxilla. — Fig. 134, first maxillipede. — Fig. 135, second pereiopod. — Fig. 136, first pleopod of Postlarva I. — Fig. 137, first pleopod of Postlarva II.

Thorax.

The carapace is now nearly as in the adult described in the literature under the name of *Amphionides*. The rostral plate is well developed and fleshy (Fig. 130) with the tiny rostrum at the tip and with the metope placed posteroventral to it. The orbital lobe and the antennal lobe of the carapace have enlarged, but they have not yet the full adult size. The carapace has further enlarged into a semiglobular shape, but its margins are still naked and its tissues are thin and paper-like, as described for *Amphionides* by GURNEY (1936).

Abdomen.

The abdomen has grown, and the cuticle has become thinner and, at least in the preserved material, is placed more loosely around the body, most likely because of shrinking of the latter, as is also the case for the thorax. When the enormous pressure under which the shrimp is living is released, the whole body gets more or less out of shape. The lateral pleura of the abdomen have enlarged, and especially medial to them the body continues ventrally as muscular lobes to which the pleopods are attached. Here again it must be remembered that the muscles are of a certain firm consistency, and possibly in the living specimens these conical muscular lobes are placed inside an ordinary plain surface; first after being transported from a pressure of more than 200 atmospheres to the surface an explosion, and later shrinkage, occur in the softer parts between the myomeres. On the first abdominal segment the lateral process (Fig. 131) on which the carapace can rest is still present.

Telson.

The telson has further elongated a little and is strongly pointed with the pair of thin hairs from the previous stage at the tip; these hairs have grown a little, but are still flexible and thin.

Appendages.

No remarkable changes have taken place in the first antenna. The two flagella have become a little stouter, and possibly they have grown in length and number of joints, but as they are all broken, this cannot be established. In the second antenna (Fig. 130) the endopodial flagellum shows the same change into a longer organ, stouter at the base. The exopodial antennal plate has widened further and is now much closer in shape to that of "*Amphionides*".

The eye, which in the previous stage was unchanged from the surface form, is in this stage about to be transformed into the adult shape. The bulb of the eye has become more bulbous, and at its mediodorsal side a small additional bulb begins to appear. This additional bulb (Fig. 130) has a small opening at the distal end, inside of which is a small, globular body with a proximally reaching nerve string communicating with the eyenerve near the base of the eyeball, shortly before both pass through the short eyestalk. In this stage this not yet functional organ is difficult to interpret, but the following stage shows that it is a developing luminescent organ. Such organs are known in some Euphausids but there they are placed more posteriorly on the eyeball or eye stalk; in these cases the longitudinal axis is placed at about 90° to the longitudinal axis of the eye, and the light produced will more or less go up, down or to the sides. Here in *Amphion* the longitudinal axis of the luminescent organ has only a very acute angle with the longitudinal axis of the eye, which means that the light is normally projected straight ahead of the shrimp, but will follow the eye if this is turned out of its normal forward-pointing direction.

The mandible (Fig. 132) is shorter, more squarish, and has only a few, diminutive teeth left. The first maxilla is reduced to a short process with one or two hairs at the side of the mouth.

The second maxilla (Fig. 133). The coxa endite and the two basale endites are further reduced, the endopod and the endites are shortened, and the endopod is less swollen. Only the exopod has increased in size, and especially the anterior-pointing lobe has widened.

The first maxillipede (Fig. 134) has a narrow coxa from which the mastigobranchia has started as an anterior lobe. The basale has still a masticatory process although this has decreased considerably in size from that of the surface-living larva. The endopod is three-jointed and the exopod has developed a large basal joint with a comb of setae along its whole lateral margin. The following joints are not very distinct except for the most distal joint.

The following two maxillipedes and the thoracopods, except the second one, are reduced further. The protopods and the endopods have still a relatively well-developed cuticle, but the exopods are the most reduced ones and possibly with a poor support of body fluid so that they are poorly nourished in their growth. Their muscles are undeveloped, they have a very thin cuticle and a weak jointing, and the length has decreased so that they are not much longer than in the reduced following stage. The fifth pereiopod has disappeared and, more remarkably, also its pleurobranchia, which just in the previous stage had reached a full development like the rest of the gills.

Only the second pereiopod (Fig. 135) is well-developed as to the protopod and endopod. The coxa is still short, but it has become thicker and conical in shape and well furnished with muscles. The basale has also enlarged in thickness and has thus become much stouter. The exopod has one well-shaped basal joint followed by a line of small, withering joints. The endopod is five-jointed and also here the joints have developed in stoutness, they are all bare except that in some specimens a reminiscence remains of the rose-spines, so well-developed in the last surface-living larva.

The first pleopod (Fig. 137) has begun an interesting development. Figs. 136 and 137 show the limb in Postlarva I and II, respectively. By comparing the two stages it is seen that in the later stage the endopod has disappeared and the exopod and the protopod have more or less coalesced at least there is no movable joint between them. Both have narrowed and the exopod has lost its setae; only small vestiges are left, as can be seen in Fig. 137. Some secondary joints or lines across the limb can be seen, and as they do not always occur in the same place I have drawn both the right and left limbs of the same specimen. In the limb to the rigth in Fig. 137 the first line, which is nearest to a jointing, is the one between the protopod and the exopod. The two further lines across the exopod cross at places where formerly two setae were placed. This can often be noticed in a growing leaf-shaped exopod or endopod with many setae, where such lines can be seen running across the joint between corresponding setae on each side of the joint. I think this developmental stage of the first pleopod shows clearly that the very elongated pleopod in the adult is built from the protopod and the exopod together.

The following four pairs of pleopods have enlarged both their protopods, exopods and endopods. On the last the appendix interna has grown into an elongate, narrow lobe separated from the endopod except at the base, much as in the following — most likely adult — stage (Fig. 155). Because the pleopods in this new deep-sea life of *Amphion* have become the only locomotory organs, the setae have increased in number and length on both exopod and endopod (see Fig. 155).

Adult or **Postlarva III**

Figs. 138–158.

Amphionides valdiviae Zimmer, 1904, pp. 225–228.
— — Gurney, 1936, pp. 397–399.
— — — 1942, pp. 223–225.

Localities.

"Dana" St.	1156	V	25°11′N,	20°57′W.	6000 m wire	6 p. m.,	E. 300,	90 min.	25.10.1921.	1 spec.
	3561	II	4°20′S,	116°46′W.	4000 m —	9 a. m.,	S. 150,	120 —	24. 9.1928.	2 —
	3676	VII	5°52′S,	131°14′E.	5000 m —	1 a. m.,	S. 150,	180 —	23. 3.1929.	1 —
	3677	II	5°28′S,	130°39′E.	4000 m —	2 p. m.,	S. 150,	180 —	23. 3.1929.	3 —
	—	III	—	—	3000 m —	2 —	S. 150,	180 —	23. 3.1929.	17 —
	3917	II	1°45′N,	71°05′E.	3700 m —	6 —	S. 150,	120 —	5.12.1929.	2 —
	3933	II	11°18′S,	50°03′E.	3500 m —	10 a. m.,	S. 150,	180 —	20.12.1929.	1 —
	3940	IV	8°24′S,	42°54′E.	200 m -	4 —	S. 200,	90 —	24.12.1929.	1 —
	3980	VII	23°26′S,	3°56′E.	5000 m —	9 —	S. 150,	120 —	17. 2.1930.	5 —
	—	VIII	—	—	4000 m —	9 —	S. 150,	120 —	17. 2.1930.	1 —
	3998	VII	7°34′S,	8°48′W.	5000 m —	7 —	S. 150,	120 —	1. 3.1930.	2 —
	—	VIII	—	—	4000 m —	7 —	S. 150,	120 —	1. 3.1930.	1 —
	—	IX	—	—	3000 m —	7 —	S. 150,	120 —	1. 3.1930.	1 —
	4000	IX	0°31′S,	11°02′W.	3000 m —	6 —	S. 150,	120 —	4. 3.1930.	2 —
	4003	III	8°26′S,	15°11′W.	4000 m —	11 —	S. 150,	120 —	9. 3.1930.	2 —
	—	IV	—	—	3000 m —	11 —	S. 150,	120 —	9. 3.1930.	1 —
	4017	II	29°11′N,	14°14′W.	4000 m —	11 —	S. 150,	120 —	27. 3.1930.	1 —
"Discovery" St.	295		5°30′N,	17°45′W.	2500—2700 m depth —	13 p. m.,	TYF	180 —	25. 8.1927.	3 —

This the last known stage in the development of *Amphion* has an interesting history. It was first described by Zimmer in 1904 as a new genus and species, *Amphionides valdiviae*, on material from the German Deep-Sea