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THE CARLSBERG FOUNDATION'S
OCEANOGRAPHICAL EXPEDITION ROUND THE WORLD 1928—30
AND PREVIOUS "DANA"-EXPEDITIONS
UNDER THE LEADERSHIP OF THE LATE PROFESSOR JOHANNES SCHMIDT

DANA-REPORT No. 77

LARVAE OF DECAPOD
CRUSTACEA
THE AMPHIONIDAE

BY
POUL HEEGAARD

WITH 165 FIGURES IN THE TEXT

PUBLISHED BY THE CARLSBERG FOUNDATION

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PREFACE

The present paper deals with *Amphion* and is the second of my "Dana" Reports (also No. 67) on the Decapod larvae.

The material for this investigation has been collected by various "Dana" and other Danish expeditions sponsored by the Carlsberg Foundation.

A list of stations on which *Amphion* larvae were caught is found at the end of the paper (p. 72). The stations are arranged in three tables (Tables XII-XIV) after their position in the three main oceans: the Atlantic, the Indian and the Pacific Oceans. The border between the Indian and the Pacific Oceans is considered to be a line from the Philippines over the Moluccan Islands and New Guinea to Kap York in Australia. The border between the Atlantic and the Indian Oceans is considered to be the waters of the Cape of Good Hope.

The station lists include serial number of stations and hauls, month, gear and duration of hauls, as well as the number of larvae caught at the different depths, here indicated as the length in meters of wire on the gear (m.w.). Finally, it is noted how these larvae are distributed among the different stages of development.

More detailed information on the collection of the material from the expeditions sponsored by the Carlsberg Foundation, Denmark, is given in the following three papers:

1. Introduction to the Oceanographic Reports. The Danish "Dana" Expeditions 1920-22. By JOHNS. SCHMIDT. Oceanogr. Rep. edited by the "Dana" Committee, No. 1, Copenhagen, 1929.
2. Introduction to the Reports from the Carlsberg Foundation's Oceanographical Expedition Round the World 1928-30. Dana-Report No. 1, Copenhagen, 1934.
3. List of Supplementary Pelagic Stations in the Pacific Ocean and the Atlantic with an Introduction by Å. VEDEL TÅNING. Dana-Report No. 26, Copenhagen, 1934.

These three papers state the purpose of the "Dana" Expeditions, and explain the sampling methods and the gear used. They also include complete lists of stations and hauls with all information on position, temperature, depth, gear, etc.

Further information on locality, bottom, temperature, depth, gear, etc. is found in the following papers:

1. "Discovery" Investigations. Station list 1925-1927. "Discovery" Report, vol. I, Cambridge, 1929.
2. "Discovery" Investigations. Station list 1929-1931. Ibid. vol. 4, Cambridge, 1932.
3. "Discovery" Investigations. Station list 1931-1933. Ibid. vol. 21, Cambridge, 1941.
4. "Discovery" Investigations. Station list 1933-1935. Ibid. vol. 22, Cambridge, 1942.
5. G. E. R. DEACON: A General Account of the Hydrology of the South Atlantic Ocean. Ibid. vol. 7, Cambridge, 1933.
6. C. M. YONGE: Origin, Organization and Scope of the Expedition. "Great Barrier Reef" Exped. 1928-29, vol. 1, no. 1, 1930.
7. F. S. RUSSEL — J. S. COLMAN: The Zooplankton. I. Gear, Methods and Station Lists. —Ibid. vol. 2, no. 2, 1931.
8. S. T. HARMER — D. S. LILLIE: British Antarctic "Terra Nova" Expedition 1910, List of Collecting Stations. — Nat. Hist. Rep. Zool. vol. II, no. 1, 1914.

The area investigated is in the Atlantic limited to the north by a line from the English Channel in the east to Florida in the west and by a line between Japan and San Francisco in the Pacific. To the south it goes round the Cape of Good Hope waters and down to Sydney, Australia and Wellington, New Zealand. The samples with *Amphion* were all taken between 36° north and 36° south.

For the pelagic fishing, wire length paid out is given in the tables as m. w. Further are noted locality, month, hour for the gear being set, and duration of the haul. The following are the abbreviations for types of gear used:

- E. 300 — open ringtrawl, 300 cm in diameter, meshes 24–18–12 mm, mouth to end.
- S. 200 — open stramin-net, 200 cm in diameter, about 400–500 strands per m.
- S. 150 — open stramin-net, 150 cm in diameter, about 400–500 strands per m.
- S. 50 — open stramin-net, 50 cm in diameter, about 400–500 strands per m.
- P. 100 — open combined stramin and silk net, 100 cm in diameter, stramin 450 strands per m., silk 23 strands per 10 mm, extra heavy grit-gauze No. 50.

In Tables XII–XIV the figures for the actual catches are given first, behind which (in boldface type) are given the same figures converted to the nearest whole number (if below 1 raised to one) for diameter 200 cm and duration 120 min.

Some specimens were so damaged that neither their exact length nor their larval stage could be determined. This causes the sum of the figures under the larval stages in the tables in some cases to be smaller than the figure for the number of specimens taken in the haul.

The figures for surface catches (sf.), both in the tables and elsewhere in the text, are not fully reliable as they are based on hauls taken with the small net S. 50, from which larvae may escape, and with a duration of 5 minutes only, which for the converted figure means that the actual catch-figures have to be multiplied by 384 to give the converted number. However, they are included to give an indication of the occurrence in the surface.

The hour given denotes the time when the gear was set and the haul began.

For the Pacific Ocean the stations 4760–4820 (Table XIV) have been taken by commercial vessels whose speed was too high during hauling. Therefore, the catches pr. hour and the fishing depth pr. m wire are not comparable to those of the standard hauls. For this reason these stations have been excluded from the calculations.

The nets are fished horizontally; the actual fishing depth for wire length less than 1000 m is approximately one third of the wire length paid out and for wire lengths of 1000 m or more, ca. one half of the wire length.

The material has been preserved in alcohol, most of it for a period of about 45 years; therefore, no information as to colour of the specimens is given. The only information on colour I know of in the literature is GURNEY'S (1936 and 1942): "the body is almost colourless, but there are red chromatophores in the mouth region, at the base of the antenna, at the base of each leg and at the base of the telson. In one specimen there was also a chromatophore ventrally in abdominal somite 5. The eye may appear blue. The peculiar swollen part in the middle of the antennal flagellum was of a blackish orange colour."

The figures accompanying the descriptions of the species are all drawn by means of a camera lucida with a scale for measurements drawn together with the figure and placed below it, or close to a group of figures all drawn at the same time and with the same magnification.

I am thankful for having been entrusted with this material which is large enough to enable me to describe nearly the complete development of *Amphion* from larva to adult. Only the sexually ripe male and female and may be the immature adult are still unknown to science. No larger changes may be expected from the previously named "*Amphionides valdiviae*" to the sexually mature specimen, or it may change into a third already known, or unknown form, representing the adult, sexually ripe shrimp.

In presenting this work it is my privilege to thank all those persons and institutions who by different means have rendered me valuable help during my work on this paper:

- Dr. ERIK BERTELSEN, "Dana" Collections, Charlottenlund Slot, Charlottenlund.
The British Museum (Natural History), London.
- Mr. J. BRUHN MØLLER, Danmarks Fiskeri- og Havundersøgelser, Charlottenlund.
The Carlsberg Foundation, Copenhagen.
The Central Institute of Zoology, University of Copenhagen.
- Mr. JENS HOLMGAARD, Zoological Museum, Copenhagen.
- Mr. R. W. INGLE, British Museum (Natural History), London.
The Library, University of Copenhagen.
- Mrs. A. NORDLUNDE, Zoological Museum, Copenhagen.
- Mrs. M. PETERSEN, Zoological Museum, Copenhagen.
- Dr. ERIK POULSEN, Danmarks Fiskeri- og Havundersøgelser, Charlottenlund.
- Mrs. E. SØRENSEN, Institute of Comparative Anatomy, University of Copenhagen.
- Prof. K. G. WINGSTRAND, Institute of Comparative Anatomy, University of Copenhagen.
- Dr. TORBEN WOLFF, Zoological Museum, Copenhagen.

AMPHION REYNAUDI H. MILNE-EDW.

- Amphion reynaudi* H. MILNE-EDW., 1832, pp. 336-340, pl. 12, Figs. 1-10.
— — — — 1837, p. 486, pl. 28, Figs. 8, 9.
— — DOHRN, 1870, pp. 607-626, Figs. 1-10.
— — CLAUS, 1876, p. 47, pl. 8, Fig. 8.
— — BOAS, 1880, p. 185.
A. provocatoris C. BATE, 1888, pp. 347, 913-918, pl. 148.
A. reynaudi C. BATE, 1888, pp. 347, 906-911, pl. 146, 147. Figs. 73-76.
A. reynaudi ORTMANN, 1893, p. 90.
A. reynaudi GURNEY, 1936, pp. 392-399, Fig. 12.
Amphionides valdiviae ZIMMER, 1904, p. 226.
— — GURNEY, 1936, p. 397.

Two species of *Amphion* have been described: *A. reynaudi* M.-EDW. from the Pacific, with rostral spine but without postrostral spine, and *A. provocatoris* BATE from the Atlantic, without rostral spine but with postrostral spine, and with a few other minor differences.

As first pointed out by ORTMANN (1893) and later by GURNEY (1936), all hitherto known specimens belong to one and the same species, which therefore must be *Amphion reynaudi* M.-EDW. All *Amphion* larvae have a rostral spine, although it is rather small and difficult to recognize in some cases, at times it may be broken. The postrostral spine, which is an anterior dorsal organ, is also present in all *Amphion* specimens, although MILNE-EDWARDS did not see and describe it for his specimen. That the postrostral spine is an anterior dorsal organ can be seen especially in the younger stages, where GURNEY (1936) describes it as "a simple protuberance".

For this reason all 5108 specimens in the "Dana" material are here described as belonging to one species, *Amphion reynaudi* M.-EDW., with a world-wide distribution throughout the tropical and sub-tropical oceans.

HISTORY

The literature on Amphionidae is filled with speculations, but unfortunately very little positive knowledge about the systematic position of the family can be gained from it.

Amphion was first described from the Indian Ocean by H. MILNE-EDWARDS in 1832, and later again in his "Histoire Naturelle de Crustacés" (1837, pp. 486-489, pl. 28, Figs. 8, 9). The figures show an old larva most likely in stage XIII, if one judges from the first antenna, but the fifth pair of pereopods, which should be present, is missing in the figure. He compares it with the Phyllosomes and the Squillid larva *Alimes*. The species was named *A. reynaudii* after its collector. MILNE-EDWARDS included *Amphion* together with *Phyllosoma* in his "Stomapodes bicuirassées" on the assumption that they were mature forms.

ANTON DOHRN (1870) also accepted it as an adult, and interpreted part of the hepatopancreas of an older *Amphion* as ovaries filled with eggs. Further, due to the four gills which he found in the specimen and wrongly interpreted as an adult character judging from littoral forms, he declared it definitely to be a sexually mature individual. After his figure (pl. 15, Fig. 2) with four pleurobranchiae and five pereopods it must be a larva in its XIII Mysis stage. DOHRN also had part of a second individual and of a younger larva (pl. 16, Fig. 10) which the figure shows to be in its third Mysis stage. His three specimens were from the

China Sea, the Indian Ocean and the Atlantic, and he suggested that they most likely represented different species, a suggestion he further considered supported by their different localities.

CLAUS (1876) insisted on the larval nature of *Amphion* and concluded that it was most closely related to the Sergestidae and *Acanthosoma*. He studied a series of stages, the earliest of which he noted to be the same as the youngest larva described by DOHRN (third Mysis). The oldest stage he figured (pl. 8, Fig. 8) shows a larva in its XIII Mysis stage. In the same year appeared a letter from WILLEMOËS-SUHM from the "Challenger", dated December 1875, in which he claimed to have caught near Australia some full-grown *Amphion* with testes. This caused CLAUS to declare in a postscript that now he was forced to accept the possibility that *Amphion* could become mature without much change of form, in which case it would represent "eine interessante Schizopoden-Form, deren Maxillen und vorderen Kieferfüsse zu den Decapoden hinführen und deren Rückenschild bereits mit sämtlichen Thoracalringen verwachsen ist" (p. 112).

BOAS (1879, 1880, 1883, 1939) stressed the opinion that *Amphion* was a larval form and supported this by the shape of the antennae and pleopods. As in Penaeidae of this developmental stage the first maxilla is a locomotory appendage but in the present larva it functions as a mouth appendage like in the Phyllosomes, the Penaeid relationship must be rejected. BOAS concluded that *Amphion* could not be a Penaeid, but hypothetically it might be the larva of *Polycheles*, provided that the sexually ripe *Amphion* is not a yet unknown crustacean.

SPENCE BATE (1888) had for his "Challenger" Report a comparatively rich material from which he described a number of stages, but he found none which could with certainty be pronounced to be adult (p. 918). He thought, however, that the adult would not differ much from the oldest larva, in which leg no. 5 was a large, uniramous rudiment. His oldest and largest specimen was from north of New Guinea (Fig. 76) and was by WILLEMOËS-SUHM (1876) described as a male because of the biramous first pleopod. This was doubted by BATE. He distinguished two species: *A. reynaudi* with rostral spine, but no postrostral spine, from the Pacific and Indian Oceans, and *A. provocatoris* without a rostral spine, but with a postrostral spine from the Atlantic.

The figures in the "Challenger" Report represent the Mysis stages I, II, V, VI, IX, XI, XIII.

BATE included *Amphion* with *Procletes*, *Icotopus*, *Hectarthropus*, and *Eretmocarid*, all larval genera, as a tribe Haplopoda, family Hectarthropidae, in the Phyllobranchiata.

KORSCHOLT and HEIDER in their "Entwicklungsgeschichte der wirbellosen Thiere", second part, pp. 461-62, edition 1892, came to the conclusion that as *Amphion* is a Zoëa larva with rudiments of phyllobranchiae it "schliesst sich an die Carididen an".

ORTMANN (1893) arrived at the conclusion that *Amphion* contained only one species and followed BOAS by considering it as the larva of *Polycheles*.

KOEPPEL (1902) attempted a thorough revision of the genus, but with inadequate material (nine specimens) and unfortunate results. He claimed it had "broad lamellae" at the base of both the third maxillipede and the pereopods 1-5 although none of his figures show these "lamellae". He further stated that the fifth pereopod is biramous and the first pleopod missing. He considered the oldest individuals as mature females related to the Sergestidae. His figures show first Mysis stage, but with telson-plate, first maxillipedes and other details incorrect, and XII Mysis stage with first antenna, flagellum of second antenna, and other details incorrect.

In 1904, ZIMMER described a new crustacean from the "Valdivia" Expedition and called it *Amphionides valdiviae*, thus indicating its close relationship to *Amphion*. No figures were supplied. The material was from the Atlantic near Madeira, off Cape Palmas and from the Indian Ocean between the Seychelles and Dar es Salam. In contrast to *Amphion*, which is a surface form, *Amphionides* was taken at about 4000 meters depth. In one of the specimens the fifth pereopod was present as an unbranched, six-jointed appendage. Zimmer regarded this specimen as a female. The other specimens without a fifth pereopod he considered as males.

C. M. SELBIE (1914) took up the problem concerning the relationship between *Eryonicus* and *Polycheles* and came to the conclusion that they were both independent species, but belonging to closely related genera.

This was discussed by O. SUND (1915) who pointed to the almost identical spination of the carapace in a number of pairs each of one species of *Eryonicus* and one of *Polycheles*. Further, members of each genus

occurred in the same geographical area, and he concluded that *Eryonicus* must be the larval form of *Polycheles*. BOUVIER (1917) argued against SUND's view. However, SUND's view has later been generally accepted.

GURNEY (1924) discussed the systematic position of *Amphion*. He supported the opinion of KORSCHOLT & HEIDER and wrote: "*Amphion* includes larval and adolescent stages of a Caridean, the adult of which is at present unknown and which is probably not referable to any existing family". In the "Discovery" Reports GURNEY (1936) published his second paper dealing with *Amphion*; it was based on 97 specimens, or about twice the number of all hitherto known specimens. He concluded that "All appear to belong to a single species", as had earlier been stated by ORTMANN in 1893. Although nothing definite could be said about the vertical distribution, his material indicated for him that "*Amphion* may be more common between 200 and 500 m. There is no indication that the larger individuals were taken in the deeper waters". — From Bermuda, GURNEY (1942) had seen a few living *Amphion*: the bodies were almost colourless but had a few red chromatophores.

In the "Discovery" material from the Atlantic were three additional specimens of *Amphionides valdiviae*. They were much damaged, but GURNEY constructed a figure of the species. He concluded that *Amphionides* is a post-larval form and suggested that it might be the adult stage of *Amphion*. As to where the two species further should be placed he wrote only: "*Amphion* and *Amphionides* must remain for the present as sole representatives of the Caridean family Amphionidae".

In his "Larvae of Decapod Crustacea" (1942) GURNEY again deals with the Amphionidae. Concerning *Amphion* nothing new is said except that the number of larval stages is probably nine. The first stage, from deep water at Bermuda, was without rostrum. Regarding *Amphionides* he now is "inclined to think that the carapace is flattened and not inflated as I had supposed". Because of the transformed first pleopod, he claims the figure from 1936 to be that of a male (1936, p. 397). "In other specimens, which are assumed to be females, 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" (1942 p. 225). Unfortunately, no figures have yet been given of this "female" and the British Museum does not possess any material which shows these characters. The material from that museum has kindly been lent to me for examination. As to *Amphion*, GURNEY writes "The systematic position of *Amphion* has been in dispute, but I am convinced that it is the larva of *Amphionides*. They are undoubtedly Caridea".

BALLS (1937) placed Amphionidae as a subfamily under the Sergestidae, but mentioned its systematic position as doubtful, referring to GURNEY.

The different aspects of *Amphion* and *Amphionides* shall be discussed later in their proper places. For a better understanding of the following descriptions, however, a few facts shall here be mentioned. Only one species of *Amphion* is known, *Amphion reynaudi* H. MILNE-EDW., and further, the specimens of *Amphionides valdiviae* ZIMMER represent different postlarval stages of *Amphion reynaudi*. No primary or secondary sexual characters in the Amphionidae have been seen; all such claims have been caused by misinterpretations. Whether the crustacean described under the name of *Amphionides valdiviae* is a sexually immature adult of *Amphion reynaudi* or whether it only is a late postlarval stage cannot be finally decided with our present knowledge, as no gonads or secondary sexual characters can be found in the existing material.

LARVAL STAGES

Promysis

GURNEY (1942, p. 223) declares: "I have seen one specimen of stage I, from deep water at Bermuda. There is no rostrum in stage I". Unfortunately, he gives no further details or figures of this stage. The stage described in the present paper, Mysis I, has a rostrum, but also so many embryonic characters that I am convinced that this youngest stage in my material must represent the first freelifving stage. If GURNEY is right

when noting a stage without a rostrum, it must be the hatching stage called Promysis, but even then, it is most likely that the rostrum would be present, but bent ventrally round the metope, and, therefore, very difficult to observe.

Mysis I

Figs. 1-10 (+ 11-13).

Development.

This larva bears much resemblance to an ordinary Caridean larva. It is first in the later stages, about the sixth Mysis stage, that the carapace flattens out, thus acquiring one of the characteristic features of the *Amphion* larva. The second and third maxillipedes with expodial swimmerets function as locomotory organs. None of the pereopods are yet present, nor any of the pleopods or the uropod.

Thorax.

The thorax is short and dorsally covered by the carapace, which anteriorly has a small delicate rostrum placed above the metope and not reaching the front border of this with its tip. The front border of the carapace has a concavity between the rostrum and the orbital spine. This spine is dorso-lateral to the eye-stalk, as shown on Fig. 14 of the second Mysis stage. Between the orbital spines is a frontal ridge on the carapace (Fig. 14). From the orbital spine the lateral border of the carapace slopes posteriorly, forming a second curve, which ends at a single antennal spine. From the antennal spine and backwards the border is smooth without spines, and its width diminishes slowly. The carapace is almost three times as long as wide, and terminates with nearly right angles.

A postrostral spine is described by some authors for later stages. Throughout its larval life *Amphion* has a vestigial anterior dorsal organ (Fig. 1), which in the older stages develops an anteriorly pointing spine (Fig. 111).

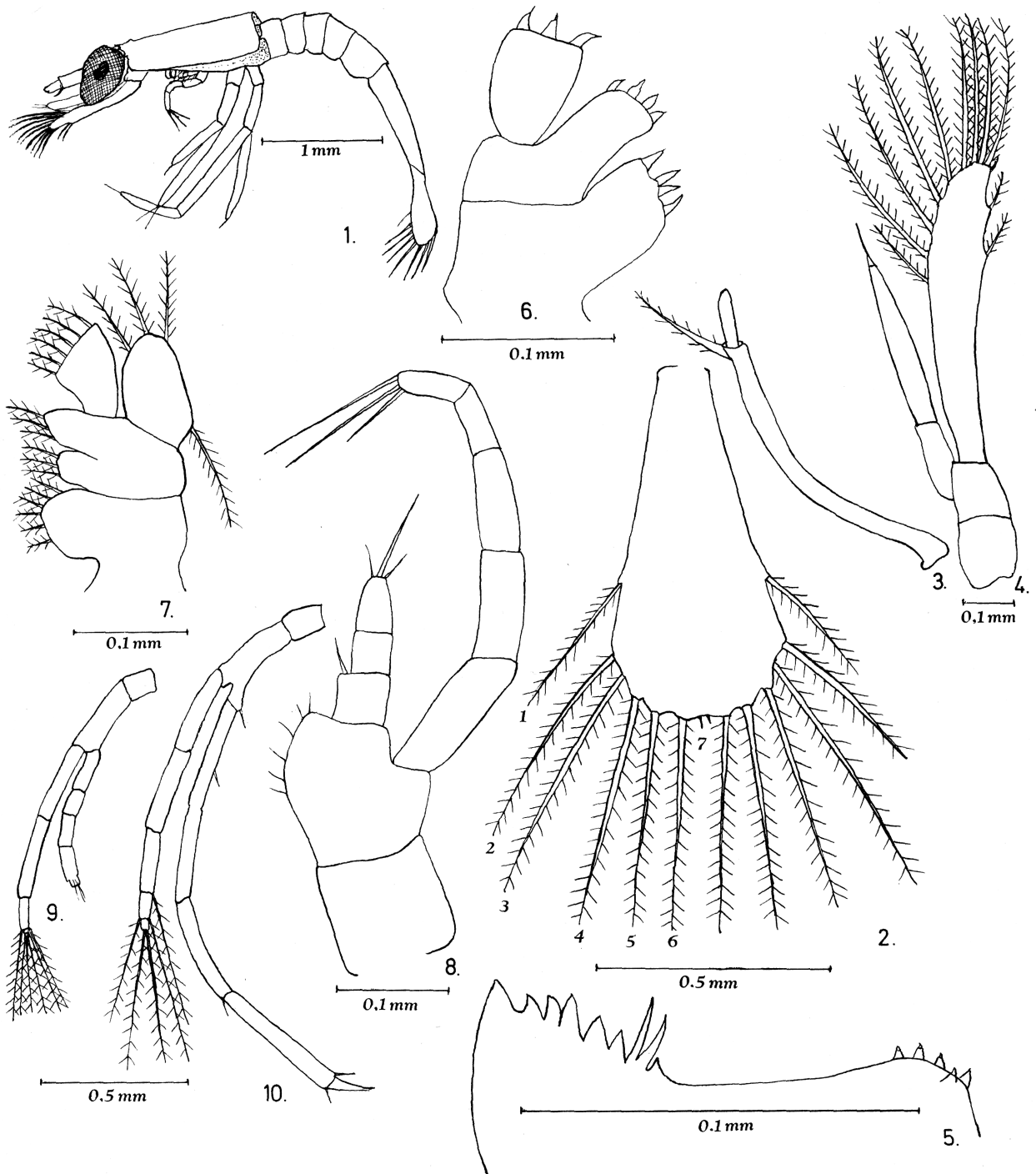
The brain is placed anteriorly between the eye-stalks, enclosed in a semiglobular capsule, the metope. The brain and its sense organs will only be very briefly mentioned because the state of preservation of the material does not allow any detailed description such as would be possible with finer dissection or histological sectioning. Inside the metope is seen a pair of conical dorsal frontal organs and ventrally a pair of smaller ventral organs. Between and behind the dorsal lobes of the frontal organ on the dorsal side of the brain is the nauplius eye. The nauplius eye is double, like two cups, with brownish pigment at the bottom, which is in the medial line of the larva. No lens was visible either in this or in any of the following larval stages. The third and medial nauplius eye if present should be placed ventrally between these cups. This could not be seen on the material. The nauplius eye neither enlarges nor develops further in any of the following 12 larval stages. This can of course only be finally confirmed through histological sectioning.

Abdomen.

The abdomen is nearly twice the length of the thorax. All six segments are without spines. The segments increase in length posteriorly, and the sixth segment is as long as segments 2-5 together. On the first segment is a lateral process, like a hook pointing forward. A similar process is common in *Brachyura* but placed on the second segment. Further, it is described from the first segment in all known Mysis larvae of *Solenocera* (HEEGAARD 1966). Its function seems to be firstly, to prevent the carapace from sliding backwards and to lift it a little free of the thorax so the gills, usually developed in the Mysis stages, are not crushed, and secondly, to provide an open space between carapace and thorax for the respiratory water to and from the gills.

Finding this process also in *Amphion*, I re-examined the Mysis larvae of *Penaeus setiferus* collected by me in 1948 and described in 1953 (HEEGAARD 1953). Figs. 11-13 show the lateral process on the first segment of the first Mysis stage viewed dorsally, laterally and ventrally. The cuticle of the dorsolateral surface of the first segment continues as a collar under which the posterior border of the carapace can become inserted and fixed.

In *Amphion* the process is spine-shaped, pointing forwards as shown in Fig. 1. Fig. 14a shows this process, together with the inserted carapace, in dorsal view.



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.

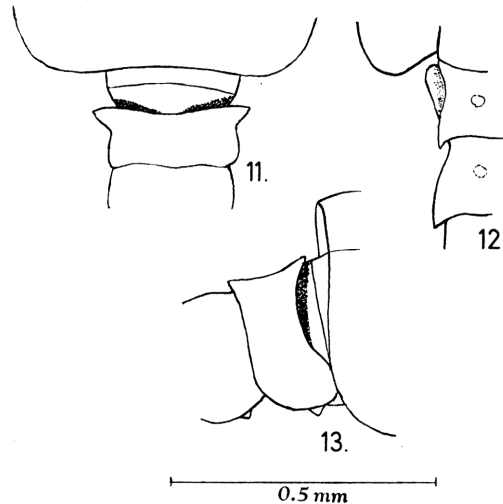
Telson.

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, plumose 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 pereopods 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.

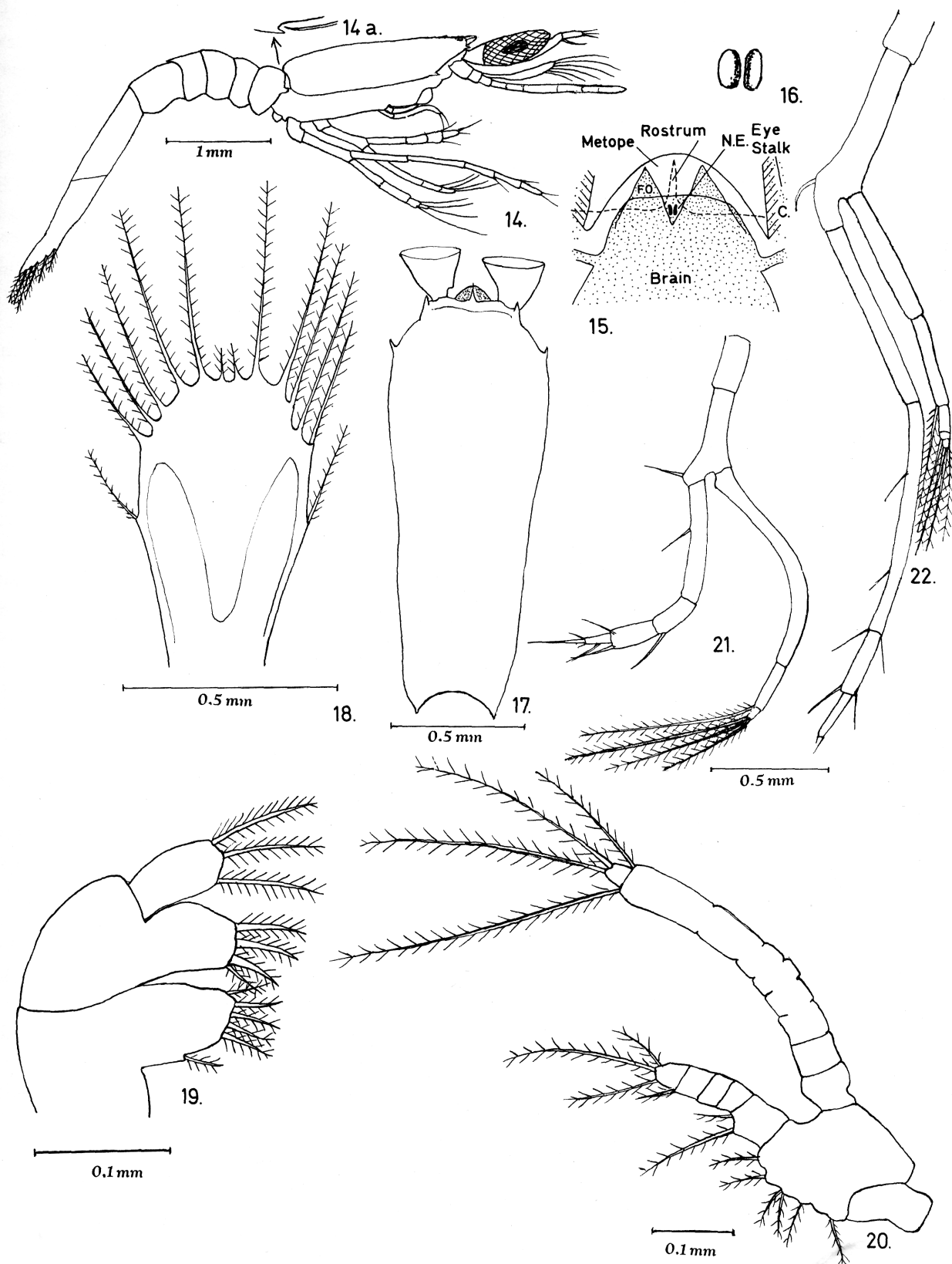
A little larger size; first antenna tipped with setae; beginning flagellum on the second antenna; setae developed on the first maxilla; coxa on first maxillipede reduced; five endopodial joints on second and third maxillipedes. First pereopod a small bud; uropod visible either under the cuticle or as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

Thorax.

The thorax and with it the carapace 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 distomedially 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 pereopods. 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 pereopods, 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 pereopods 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 pereopod. 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 pereopod 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 pereopod 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.

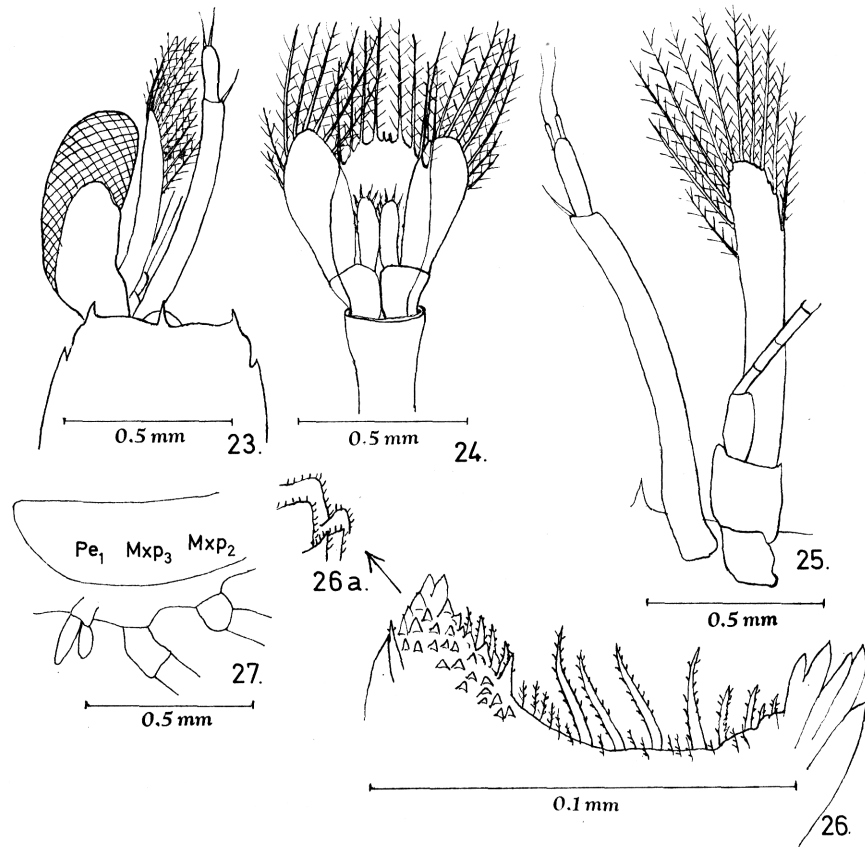
Telson.

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 pereopod 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 flagellar 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 pereopod has only developed a little further.

Thorax.

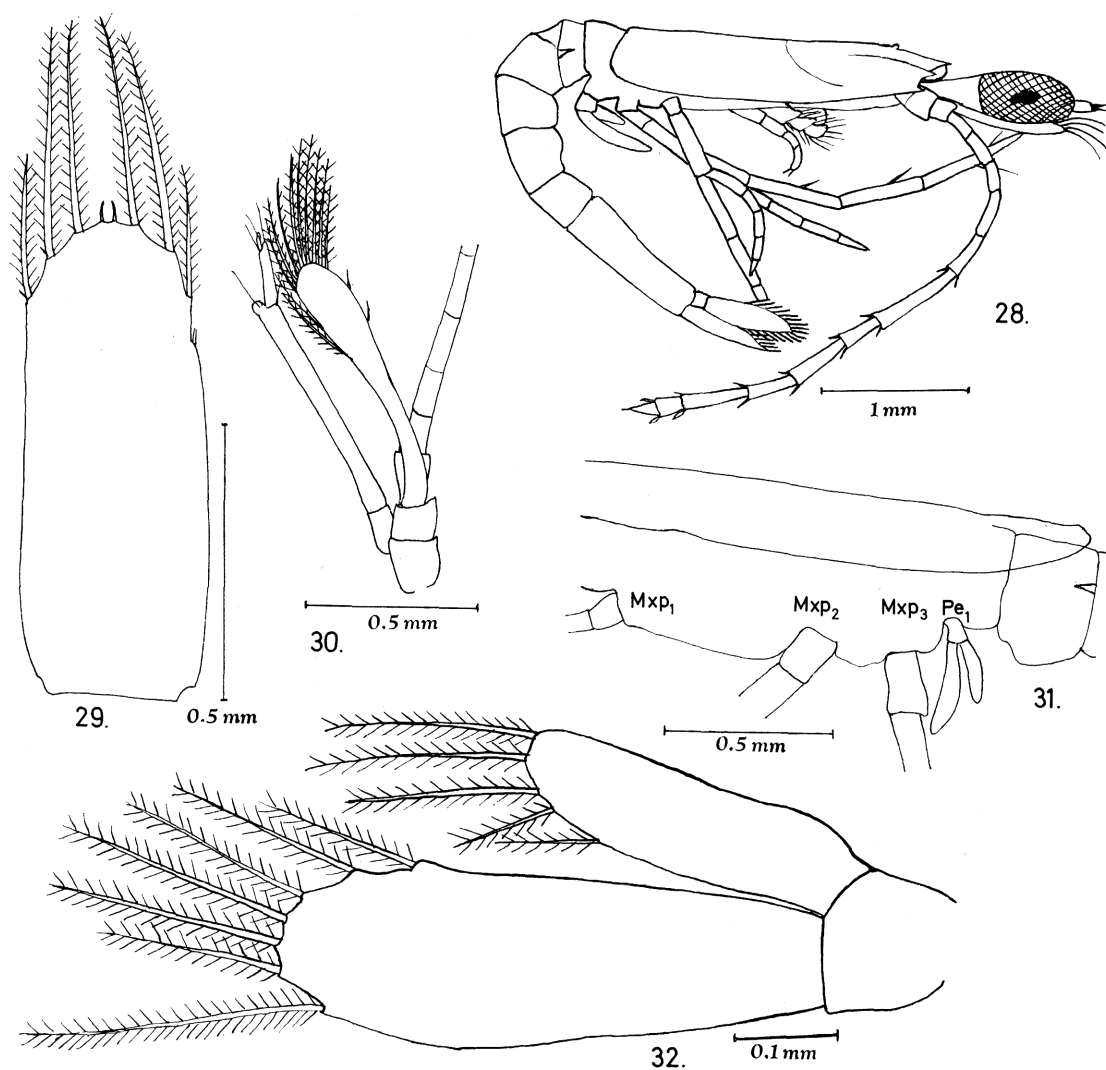
The carapace seems a little more flattened and has developed a keel running backwards from the orbital spine for about two thirds of the distance to the cervical groove, this latter being now more pronounced (Fig. 28).

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 pereopod is a little larger, especially its two branches, but no more joints have been added.

The uropods (Fig. 32) have changed. The exopod is much more elongate with nearly parallel lateral margins. The endopod has enlarged to about two thirds the length of the exopod, and it has now become functional. The endopod is furnished with few, but well-developed, plumose setae.

Dimensions.

Total length 6 mm; length of carapace 2.2 mm, width of same 0.8 mm; rostrum 0.1 mm; abdomen 2.6 mm; telson 0.8 mm.

Mysis V

Figs. 33-43.

Development.

The thorax has elongated and the carapace has become more flat, like a horizontal sail over the thorax. In a cross-section the carapace and the thorax now form a semi-circle which is dorsally convex. The abdomen is unchanged. The telson plate itself is unchanged, but its setae are reduced further, nos. 4 and 7 have shortened. First and second antenna are stronger, eye and eye-stalk larger. First maxillipede has a larger gnathobasal crista on the basale and an exite on the coxa. The first pereopod is as large as the second maxillipede, the second pereopod is present as a small bud. The uropod is nearly fully developed with a latero distal hooked spine on the exopod and a functional endopod.

Thorax.

The thorax and carapace have continued to flatten out.

Abdomen.

Unchanged.

Telson.

A further reduction has taken place in its setae (Fig. 34). Seta no. 4 is still plumose, but very short. Nos. 5 and 6 are unchanged and still long and plumose. No. 7 is shorter.

Appendages.

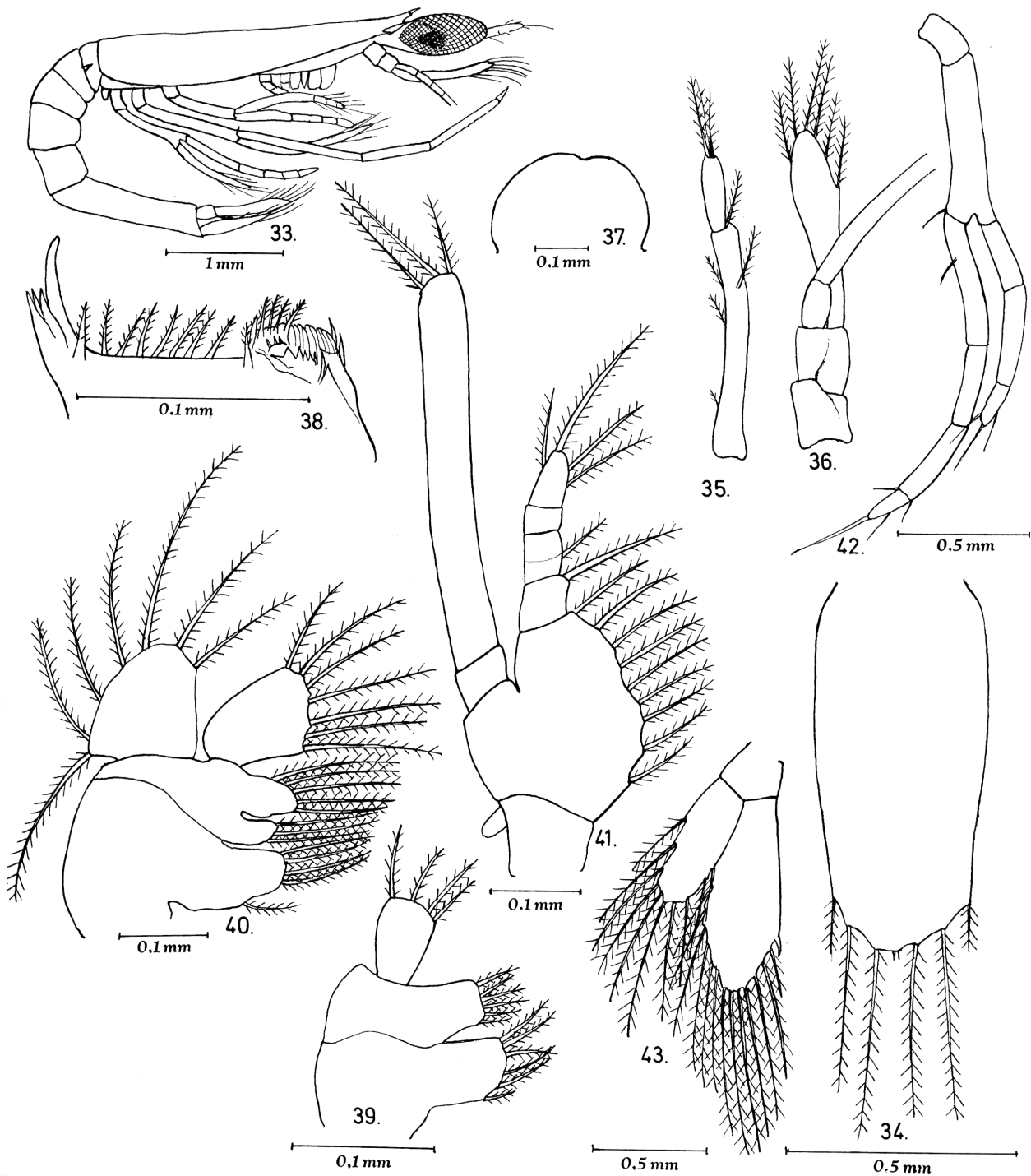
The first antenna (Fig. 35) has still only two joints, both of which have grown stronger. The distal one represents the flagella. Some plumose spines have developed on the basal joint, both along the lateral and medial margins, and the new distolateral spine from the last stage has grown in size, but is still a normal, straight, plumose seta.

Also the second antenna (Fig. 36) is stronger, and both protopodial joints have developed a longitudinal furrow with inside apodemes for the muscles, like a double stem, one part for the exopod and another for the endopod. The endopodial flagellum is stronger at the base. As it is always broken on the captured specimens its length cannot be determined. The compound lateral eyes have enlarged, especially the eye stalks, pushing the elliptical eyeball forward. The labrum (Fig. 37) is a semicircular plate with an incision in the middle of its margin.

The teeth of the mandible (Fig. 38) have developed further. The primary incisor teeth are more compressed, the secondary ones are still plumose, showing their origin, but they seem more chitinised, a little stouter and more straight. Also the molar teeth are changed, starting as individual and separated cones they have now broadened, reached each other and through reciprocal pressure become leafshaped. Between them and on the inside to them have grown ordinary "incisor" plumose spines, but these disappear again. These spines are only found on the border between incisor and molar part and seem to indicate a temporary overlapping of the two parts.

The labium is still very small, with its two lobes far apart.

The first maxilla (Fig. 39) is divided into coxa and basale, each with a masticatory medial lobe of nearly equal size. The coxa-endite is still slightly larger than the basi-endite, but both have stiff, plumose setae of



Figs. 33–43. *Amphion reynaudi*, Mysis V. Fig. 33, in total from lateral. — Fig. 34, telson plate. — Figs. 35–36, first and second antenna. — Fig. 37, labrum. — Fig. 38, incisor and molar edge of mandible. — Figs. 39–40, first and second maxilla. — Fig. 41, first maxillipede. — Fig. 42, first pereopod. — Fig. 43, uropod with exopod larger than endopod.

medium length. The endopod is now fully turned 90° . In the second Mysis the endopod was parallel with the endites on the coxa and basale, now it is at a right angle to them with its longitudinal axis in prolongation of the protopod. While in the earlier stages the endopod appeared to function together with the protopod endites, now it has a more separate function in pushing the food particles forward. The endopod has developed a fourth seta.

The second maxilla (Fig. 40) has also started to change. The coxa seems to dominate but it still has only a single lobe, and also the basale still has two lobes as in the previous stages. The endopod is turned medially,

not distally as on the first maxilla, and functions as the fourth masticatory lobe. All four "lobes" are furnished with very long plumose setae on their medial margins. The exopod is still turned forward; it has only its anterior lobe, but most lateroposteriorly a backward-pointing lobal part has started to develop.

The first maxillipede (Fig. 41) has the coxa reduced to a stalk and the basale is enlarged. The coxa has a small, lateral, fleshy lobe near the border to the basale; this will later develop into a gill. The medially pointing crista on basale is larger, strongly chitinised and lined with stiff, plumose setae. The exopod is a long, flexible rod. *Its five joints seem to have coalesced, only the first joint is clearly delimited from the rest.* On the distal tip of the exopod are three long, stiff plumose setae. In the endopod joints 2 and 3 are coalesced, but the spine on the disto-medial edge of no. 2 is still present. The tip has 4 stiff setae. The second and third maxillipedes are unchanged; the third maxillipede is the largest.

The first pereopod (Fig. 42) is now a functional limb although not fully developed. The protopod consists of a short coxa, about twice as long as wide, and a much longer basale, more than five times as long as wide. The endopod is the most fully developed of the two branches. It is four-jointed with the three first joints long and fully developed, but with joint 4 short and tipped with a strong seta. On some of the other joints are placed a few setae. The exopod is three-jointed with a few plumose, swimming setae on the last joint. The second pereopod is only a tiny bud.

The uropod (Fig. 43). The first lateral seta on the exopod has been replaced by a hooked spine, and the number of setae on the medial margin has increased. The endopod which in the previous stage had only a few setae on the tip and the disto-medial margin has now setae also on the lateral margin.

Dimensions.

Total length 6.5 mm; length of carapace 2.7 mm, width of same 1 mm; rostrum 0.1 mm; abdomen 2.6 mm; telson 0.8 mm.

Mysis VI

Figs. 44-52.

Development.

Last abdominal segment elongated. Teeth on mandible further developed; endopod on first maxilla more narrow; endopod of first maxillipede three-jointed. Second pereopod bifurcate with two-jointed protopod, but still nonfunctional.

Thorax.

The thorax and carapace have widened a little more.

Abdomen.

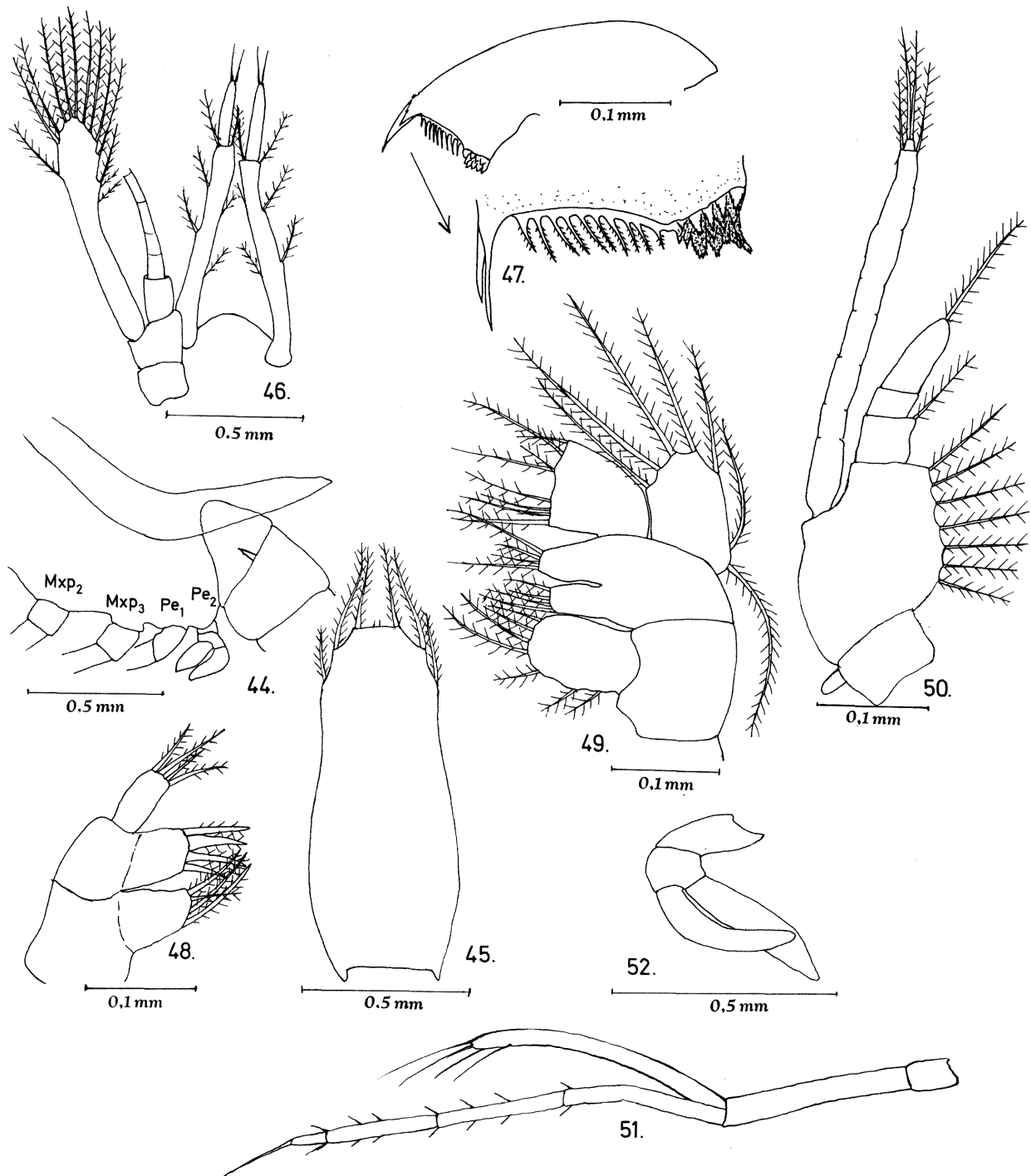
The last segment is now about six times as long as wide.

Telson.

The plate (Fig. 45) has grown to a length of 1 mm, but the setae are practically unchanged; perhaps the small setae no. 7 have become a little shorter before disappearing in the following stage.

Appendages.

The first antenna (Fig. 46) remains stout. It has now developed three setae placed with equal distances on each side of the proximal joint medially and laterally. On the mandible (Fig. 47) the secondary incisor teeth are shorter and stronger and the molar part seems more compact. In the first maxilla (Fig. 48) the setae on the basi-endite are fewer but they are more conical, and the endopodial joint is slimmer and tipped with four stiff setae. The second maxilla is shown in Fig. 49. In the first maxillipede (Fig. 50) the crista on the basi-endite has enlarged. The endopod has from now on only three joints, as joints nos. 2 and 3 have coalesced as have nos. 4 and 5. The exopod has only one small distal joint, the rest is ringed and without clear articulation.



Figs. 44–52. *Amphion reynaudi*, Mysis VI. Fig. 44, posterior part of thorax and anterior part of abdomen. Fig. 45, telson plate. — Fig. 46, metope and first and second antenna from ventral. — Fig. 47, mandible. — Figs. 48–49, first and second maxilla. — Fig. 50, first maxillipede. — Fig. 51, first pereopod. — Fig. 52, second pereopod.

The first pereopod (Fig. 51) is now the longest of the appendages. Short setae are placed along the endopod. The second pereopod is short, bifurcate, nonfunctional (Fig. 52). The protopod is divided into a longer coxa and a shorter basale, and the exopod and endopod are leaf-shaped. The uropod is almost unchanged.

Dimensions

Total length 7 mm; length of carapace 2.8 mm, width of same 1.2 mm; rostrum 0.1 mm; abdomen 3 mm; telson 0.8 mm.

Mysis VII

Figs. 53-57.

Development.

The carapace has widened and has now the shape typical for an older *Amphion*. Only two pairs of setae, nos. 5 and 6, are left on the telson which has started to narrow distally. The medial flagellum of the first antenna is showing as a small bud. Second pereopod functional, but not yet with full length. Third pereopod a small bud. The endopod of the uropod reaches the tip of the telson plate.

Thorax.

The thorax has become longer and the carapace wider so that the larva from now on has the typical shape of an older *Amphion*. The convoluted lobes of the hepatopancreas have appeared and are best developed in the anterior part of the thorax. These branched lobes which are characteristic for and only found in *Amphion* and the *Phyllosoma* larva have, together with the similarity in the thoracopods and mouth appendages caused some earlier investigators to see a close relationship between these two larval forms.

Abdomen.

The last abdominal segment has become stouter and is as long as the anterior five abdominal segments together (Fig. 54).

Telson.

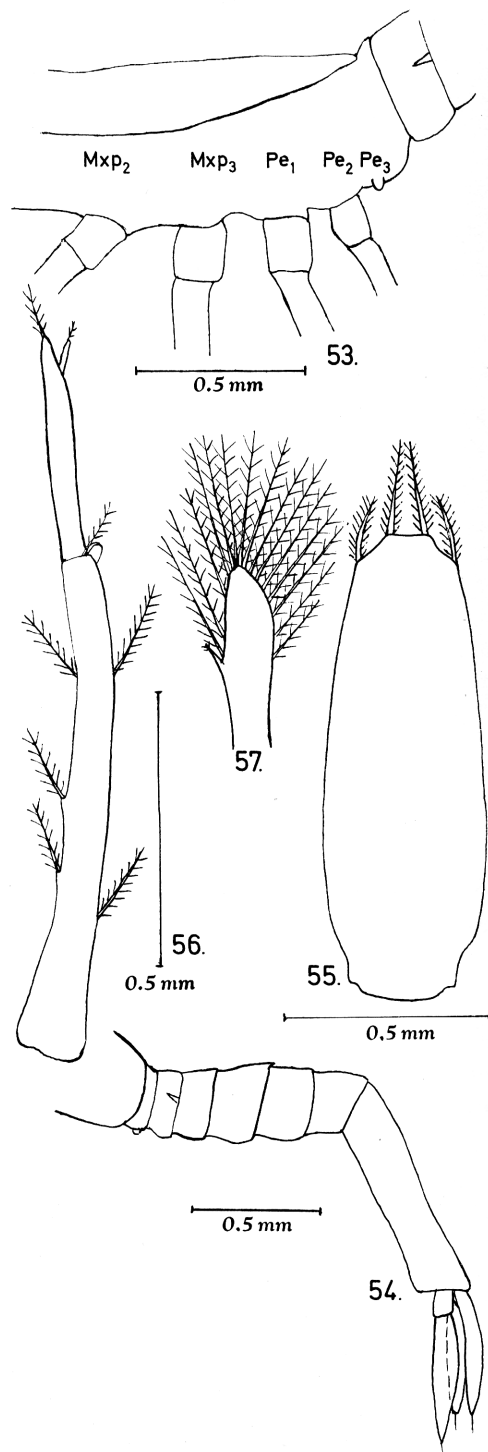
The telson plate (Fig. 55) has enlarged a little, its length being three times its largest width. The plate has started to narrow distally. The number of setae is reduced, as both nos. 4 and 7 have disappeared and 5 is reduced to half its earlier length.

Appendages.

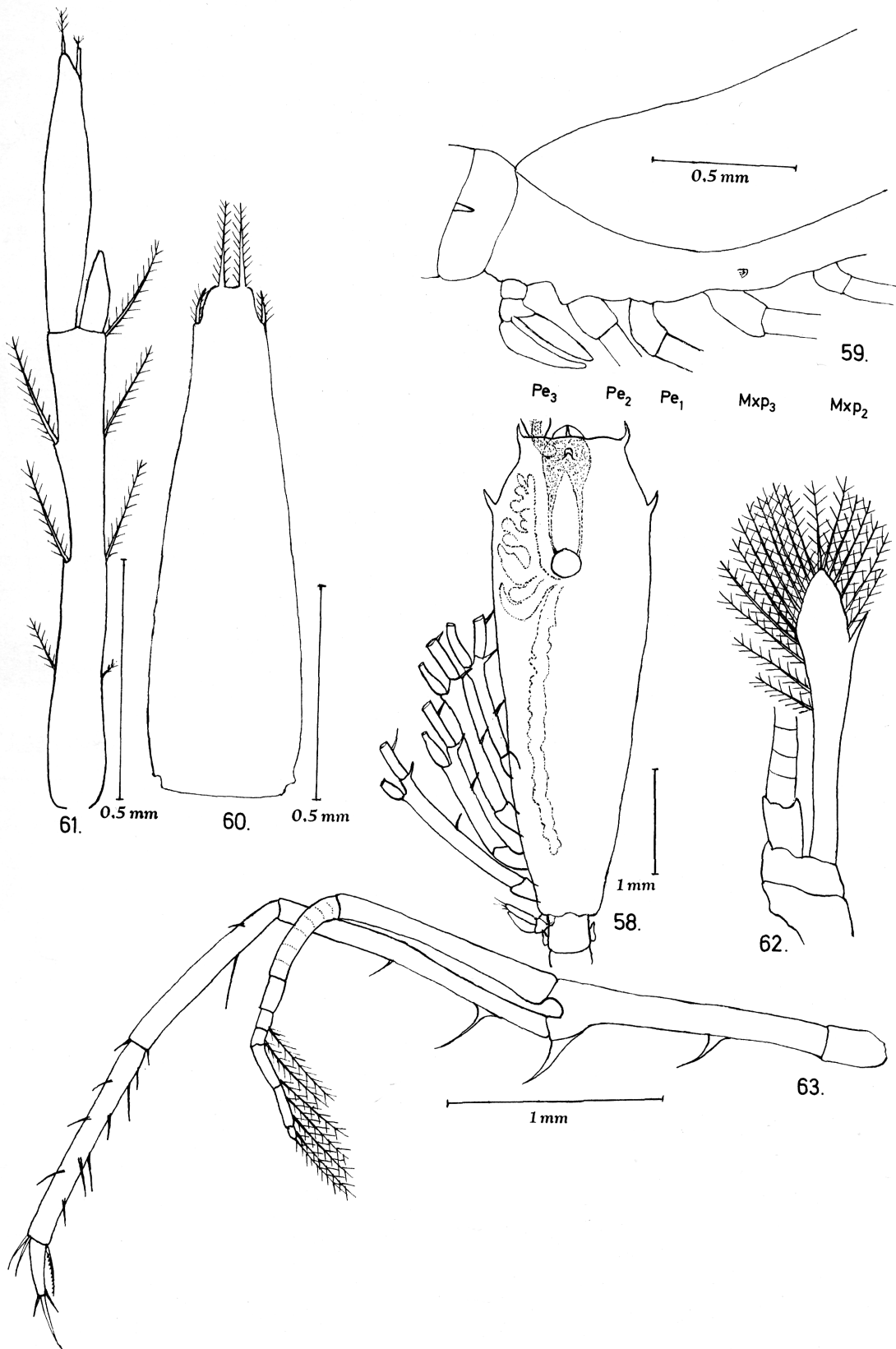
The first antenna (Fig. 56) has grown in length and stoutness and the unjointed lateral flagellum has elongated. The medial flagellum has appeared, but only as a small bud. In the second antenna the most lateroposterior of the setae on the antennal scale (Fig. 57) has changed into the antennal spine, but its former existence as a seta is still indicated by a tuft of small hairs at the tip. The second pereopod has grown to a little more than half the length of the first pereopod. The protopod has elongated, with the basale now reaching nearly its full length. The exopod has long plumose swimming setae and is locomotory. The endopod is divided into five shorter joints and is nearly twice as long as the exopod. The third pereopod appears as a small bud. On the uropod the exopod and endopod have developed a little further.

Dimensions.

Total length 8 mm; length of carapace 3.5 mm, width of same 1.5 mm; rostrum 0.1 mm; abdomen 3.2 mm; telson 1.1 mm.



Figs. 53-57. *Amphion reynaudi*, Mysis VII. Fig. 53, posterior part of thorax and anterior part of abdomen. — Fig. 54, abdomen, telson and left uropod. — Fig. 55, telson plate. — Fig. 56, left first antenna from dorsal. — Fig. 57, distal part of antennal scale.



Figs. 58–63. *Amphion reynaudi*, Mysis VIII. Fig. 58, carapace and first part of abdomen from dorsal, showing metope, brain with anterior dorsal organ, oesophageal commissura hepatopancreas, proximal part of limbs and lateral process. — Fig. 59, posterior part of thorax and first part of abdomen. — Fig. 60, telson plate. — Fig. 61, first left antenna from dorsal. — Fig. 62, part of second antenna. — Fig. 63, third maxillipede.

Mysis VIII

Figs. 58-63.

Development.

Elongation of thorax and carapace; development of hepatopancreas; reduction in setae on telson; a posterior narrowing of the telson plate. Growth of the medial flagellum of first antenna; further developments of pereopods. Third pereopod nonfunctional but with two-jointed protopod and leaf-shaped exopod and endopod; rudimentary gill on third maxillipede and in some larvae also on first pereopod.

Thorax.

The thorax (Fig. 58) is more elongate. The hepatopancreas is more branched with a main lobe consisting of a stem with blind, lateral branches running from the front intestine to near the front of the thorax. On each side an unbranched hepatopancreas lobe runs backwards to near the posterior border of the thorax.

Abdomen.

Unchanged.

Telson.

The telson plate (Fig. 60) has narrowed posteriorly; in the first third of its length its sides are nearly parallel, but in its posterior two thirds they narrow towards the tip. This can also be seen in the setae no. 5 which, besides being shorter, now are situated nearly in line with number six.

Appendages.

In the first antenna (Fig. 61) the lateral flagellum has grown much stouter; especially the tip with the two aesthetascs has widened, and also the medial flagellum has grown from a tiny bud to a lobe about three times as long as wide. The antennal spine on the antennal scale of the second antenna (Fig. 62) has lost its last setae, and is now definitely developed as a spine.

From the second maxillipede to the second pereopod the typical catching basket is developing with large spine-like "rose thorns" on the basale and the inner margin of the endopod (see Fig. 63). This basket is known for different pelagic decapods as *Phyllosoma* larvae and *Cerataspides longiremis*. It is only found in true pelagic Crustacea and must be very effective in catching pelagic organisms, partly as a trap, partly as an active apparatus. The second pereopod (Fig. 58) is now fully developed, but the third pereopod (Fig. 59) is still nonfunctional. It has a two-jointed protopod with two equally large joints, the coxa and the basale and an unjointed, but lobed exopod and endopod. A small gill bud has developed at the base of the third maxillipede and in some specimens also at the first pereopod. This is the first larval stage in which the beginning of the gill development can be observed.

Dimensions.

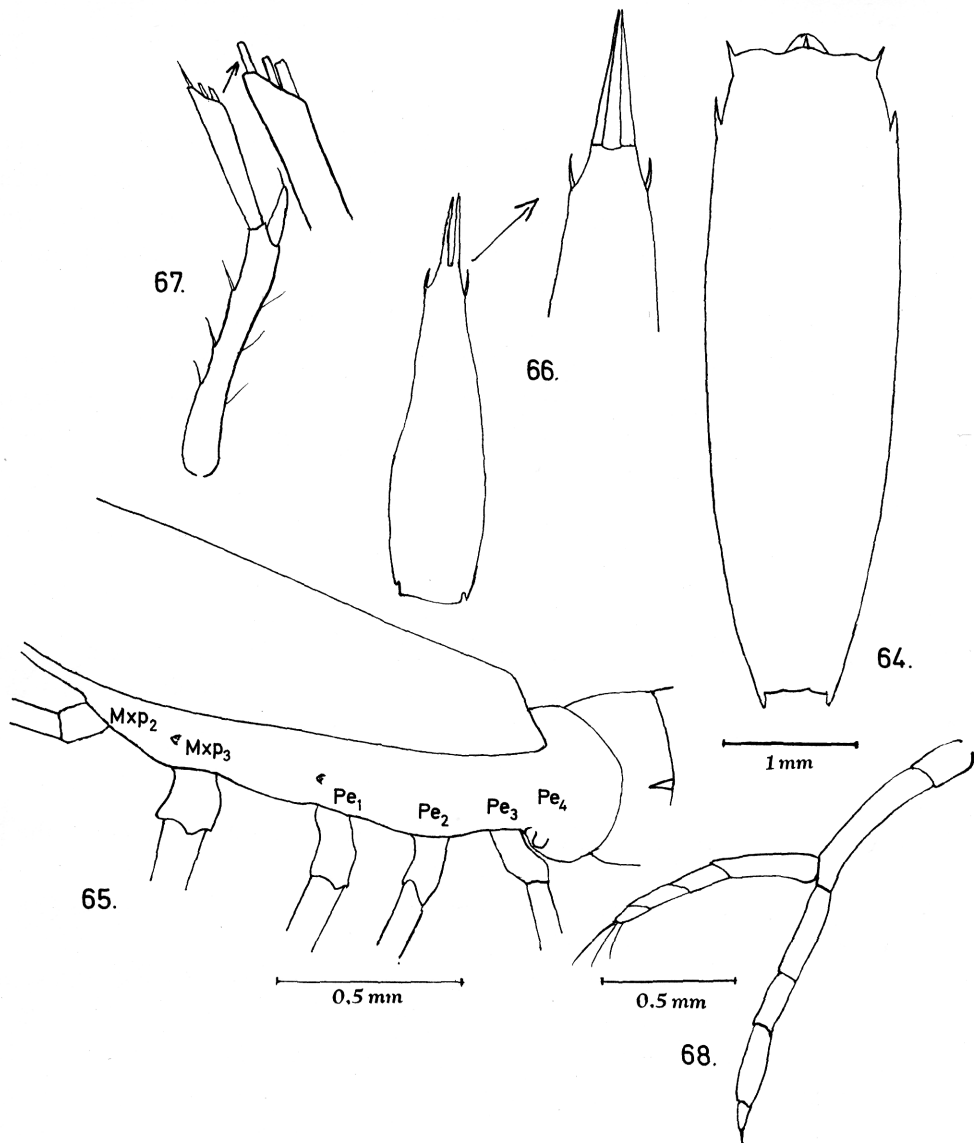
Total length 9 mm; length of carapace 4.5 mm, width of same 1.6 mm; rostrum 0.1 mm; abdomen 3.2 mm; telson 1.2 mm.

Mysis IX

Figs. 64-68.

Development.

Carapace longer and more widened posteriorly, where it ends in two small lateral lobes pointing backwards. The telson plate further narrowed posteriorly, seta no. 5 more reduced. Lateral flagellum of first antenna broader distally and with three aesthetascs; the medial flagellum is tipped with one seta. Third pereopod half as long as second pereopod, the fourth pereopod present as a small bud. Rudimentary gill-buds at the base of the third maxillipede and first pereopod.



Figs. 64-68. *Amphion reynaudi*, Mysis IX. Fig. 64, carapace and metope from dorsal. — Fig. 65, posterior part of thorax and anterior part of abdomen. — Fig. 66, telson plate. — Fig. 67, left first antenna from dorsal. — Fig. 68, third pereiopod.

Thorax.

The thorax and carapace (Fig. 64) have further elongated and the widening and flattening of the carapace has reached farther backwards. The carapace has two small posterolateral lobes pointing backwards, which gives a more free movement between thorax and abdomen during the coming stages where a further development of the abdomen takes place.

Abdomen.

The development has up to and including stage IX been very slow with little or no growth.

Telson.

The telson is still more narrow and pointed distally and seta no. 5 still smaller (Fig. 66).

Appendages.

In the first antenna the two flagella have developed (Fig. 67). The lateral flagellum has widened distally; it is still unjointed but more flattened. The medial flagellum has a small seta on the tip. The catching basket

shaped by the two last maxillipedes and the thoracopods has developed, and the third pereopods are closing the basket posteriorly. On the third pereopod (Fig. 68) the basale has grown to about three times the length of coxa. The exopod is jointed but not with distinctly delimited joints, and it is furnished with only a few small setae at the tip. The endopod is a little longer than the exopod, its joints nos. 1 and 3 are the longest. In the next stage no. 3 will be divided into two joints, when the endopod reaches its full length. The fourth pereopod is present as a small bud. Small gill buds are present at the base of third maxillipede and first pereopod.

Dimensions.

Total length 9.5 mm; length of carapace 5 mm; width of same 1.6 mm; rostrum 0.1 mm; abdomen 3.2 mm; telson 1.2 mm.

Mysis X

Figs. 69-80.

Development.

Telson is still more pointed posteriorly, with only setae no. 6 and vestigial no. 5. Labrum circular in outline with a notch in the medial line. Mandible furnished with a line of long secondary incisor teeth. Endopod of first maxilla reduced. The exopodial leaf of second maxilla enlarged with a backwards-pointing lobe. First maxillipede with coxa reduced, mastigobranchiae enlarged, basale with growing masticatory endite, endopod more setose. Third pereopod developed in length and shape as the anterior ones. Fourth pereopod half as long and now closing the catching basket posteriorly. All five pleopods developed as small buds.

Thorax.

The thorax and its carapace have grown in length and width, and the posterolateral lobes, which in the previous stage were more pointed, are now more rounded.

Abdomen.

The abdomen (Fig. 80) has grown a little and the pleurae have started to develop a free lobe for covering and protecting the growing pleopod buds.

Telson.

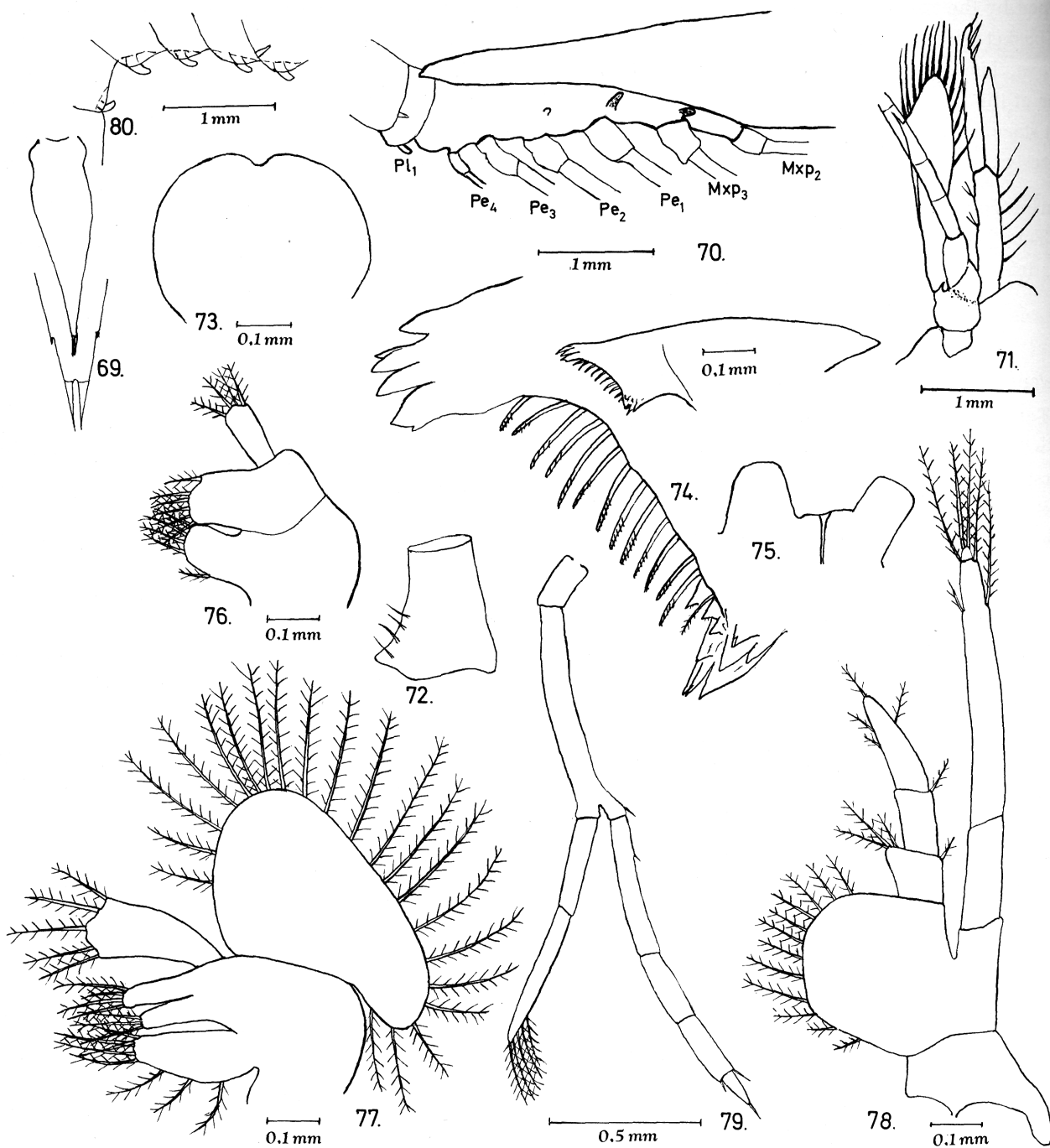
The telson is further pointed posteriorly, and the sixth pair of setae has become very short; in some specimens a tiny vestige of no. 5 can still be noticed; in others it is absent (Fig. 69).

Appendages.

The protopod of the first antenna has at the base of its curved lateral margin (Fig. 72) a line of stiff setae where the opening for the statocyst should be. Farther up on the lateral margin (Fig. 71) are two small groups of sensory hairs and on the medial margin is a line of stiff plumose setae. Both flagella have enlarged, but are still unjointed; the lateral flagellum has grown most on its lateral side so that the three aesthetascs which in stage IX were placed at the square-cut distal end, now are placed distally on the medial margin. On the basale of the second antenna (Fig. 71) the small process of stage IX at the base of the flagellum has developed to a clearly hook-shaped spine. The flagellum is stouter at its basal part and has probably (all flagella were broken off near the base) developed more joints. The labrum is now a circular plate with a small incision in the middle of the margin (Fig. 73).

In the mandible the corpus mandibulae has elongated; the primary incisor teeth and the molar teeth have been compressed towards the margins and the area of the secondary incisor teeth is much enlarged. The secondary incisor teeth stretch now over two thirds of the cutting-edge, leaving only 1/6 each to the primary incisor teeth and the molar teeth. The secondary incisor teeth, placed at the medial margin, are long and styli-form with stiff hairs on the distal third of their length (see Fig. 74). These teeth seem flexible at their base but only in a direction parallel to the cutting edge. They seem to function excellently for grating. No palp develops on the mandible.

The labium is short with two small, squarish horns (Fig. 75), separated by a medial plate and forming an angle of about 120° to this plate.



Figs. 69–80. *Amphion reynaudi*, Mysis X. Fig. 69, telson plate. — Fig. 70, posterior part of thorax and anterior part of abdomen with gills and basal part of limbs. — Fig. 71, first and second antenna. — Fig. 72, basal part of left first antenna from dorsal. — Fig. 73, labrum. — Fig. 74, mandible. — Fig. 75, labium. — Figs. 76–77, first and second maxilla. — Fig. 78, first maxillipede. — Fig. 79, fourth pereopod. — Fig. 80, ventral part of abdomen showing beginning pleopods and beginning pleural plates.

The first maxilla (Fig. 76) is comparatively reduced in size, the setae on the basiendite are less stout; the numbers of setae on coxa- and basi-endite have increased a little; they are now more like a brushing organ and not a tearing and cutting organ as in Mysis VI. The endopod is still more reduced and has only 4 distal setae.

On the second maxilla the coxa-endite, the two basi-endites, and the endopod have become more narrow, like fingers, with a brush of plumose setae on their tips. On the exopod the backwards-turning corner has begun to form a lobe pointing posteriorly (Fig. 77).

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 pereopods, 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 pereopod have grown but are still compact in shape and unbranched. A small gill-bud has developed at the base of the second pereopod 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 pereopods 1 and 2 have grown to functional size, that on the first pereopod is the best developed. A gill bud has appeared at the base of the third pereopod. 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 variation 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 Euphausiids 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.

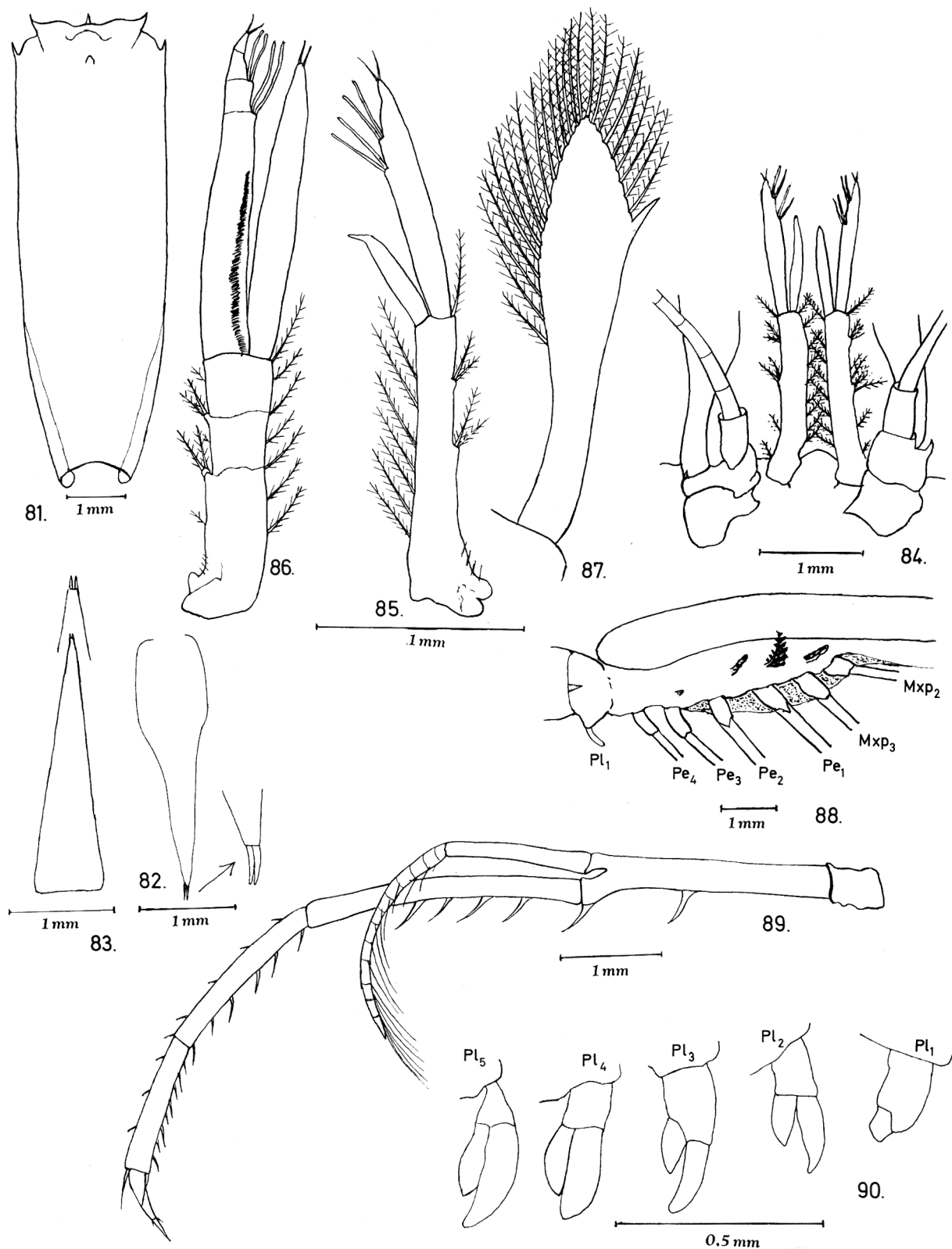
In the least-developed larvae only little change from the previous stage has taken place in the first antenna (Fig. 85); it is a little stouter, the two groups of setae on the lateral side of the stem are stiff, plumose spines, and further on the medial side of the lateral flagellum two groups each of 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 pereopod, 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 pereopod, 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 pereopods have developed to functional size. In the least developed larvae (Fig. 88) the gill on the first pereopod has free lateral branches on the stem, like the rami of a feather. The gills on third maxillipede and second pereopod have not developed so far but look more like a foxtail. A gill-bud is seen on the third pereopod. In the more advanced specimens all three first gills are feather-shaped, but the gill on the third pereopod 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.

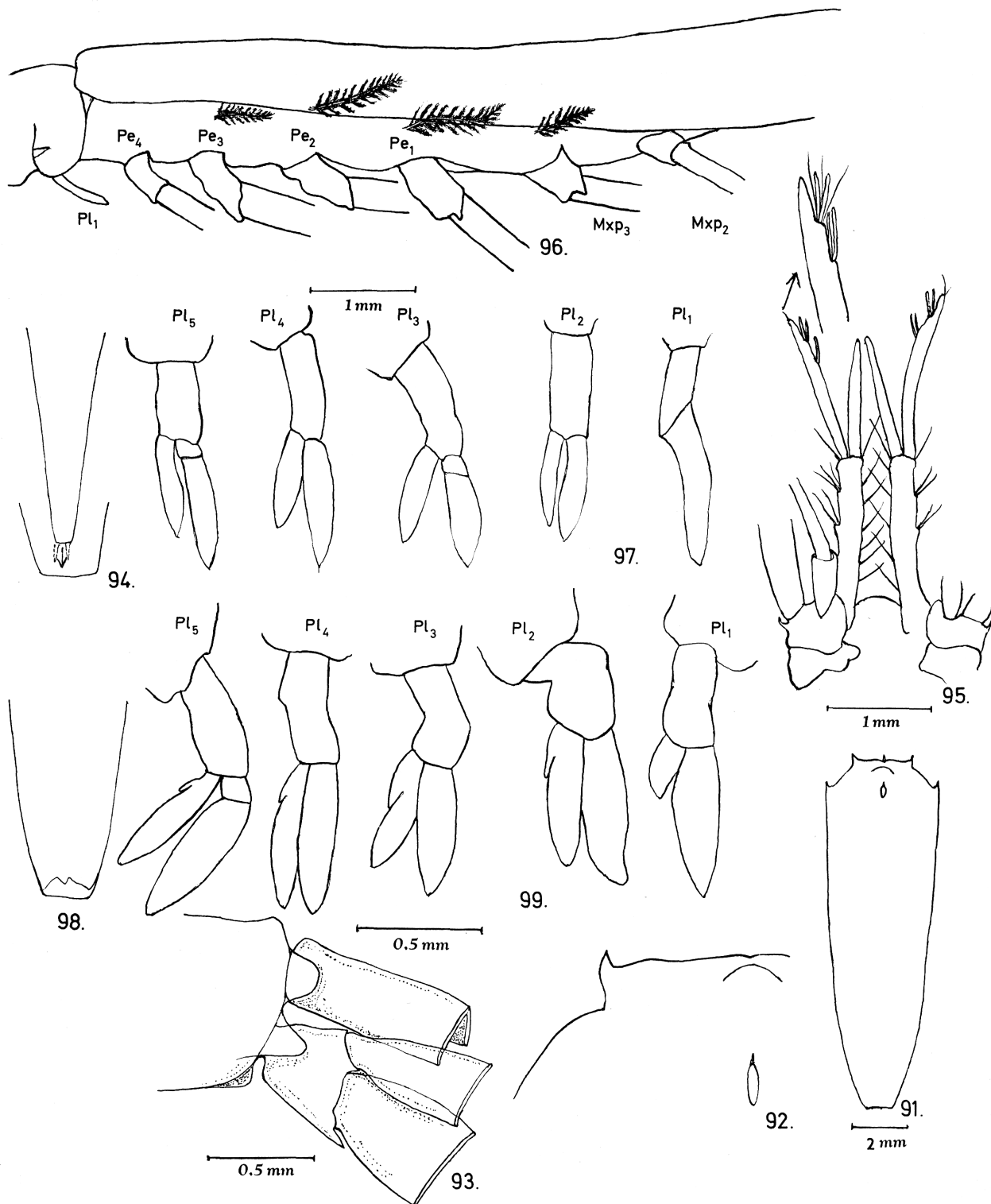
From stage X to XI especially the abdomen became enlarged, but from XI to XII again both the thorax and abdomen show the main part of the enlargement. The anterior dorsal organ is pointed anteriorly with a short spine. The fourth pereopod reaches nearly the size of the preceding ones. The number of gills 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 pleopods.

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, pereopod is now nearly as large as the preceding one. Of the fifth pereopod 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 pereopod. Thus the second maxillipede and the fourth pereopod 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

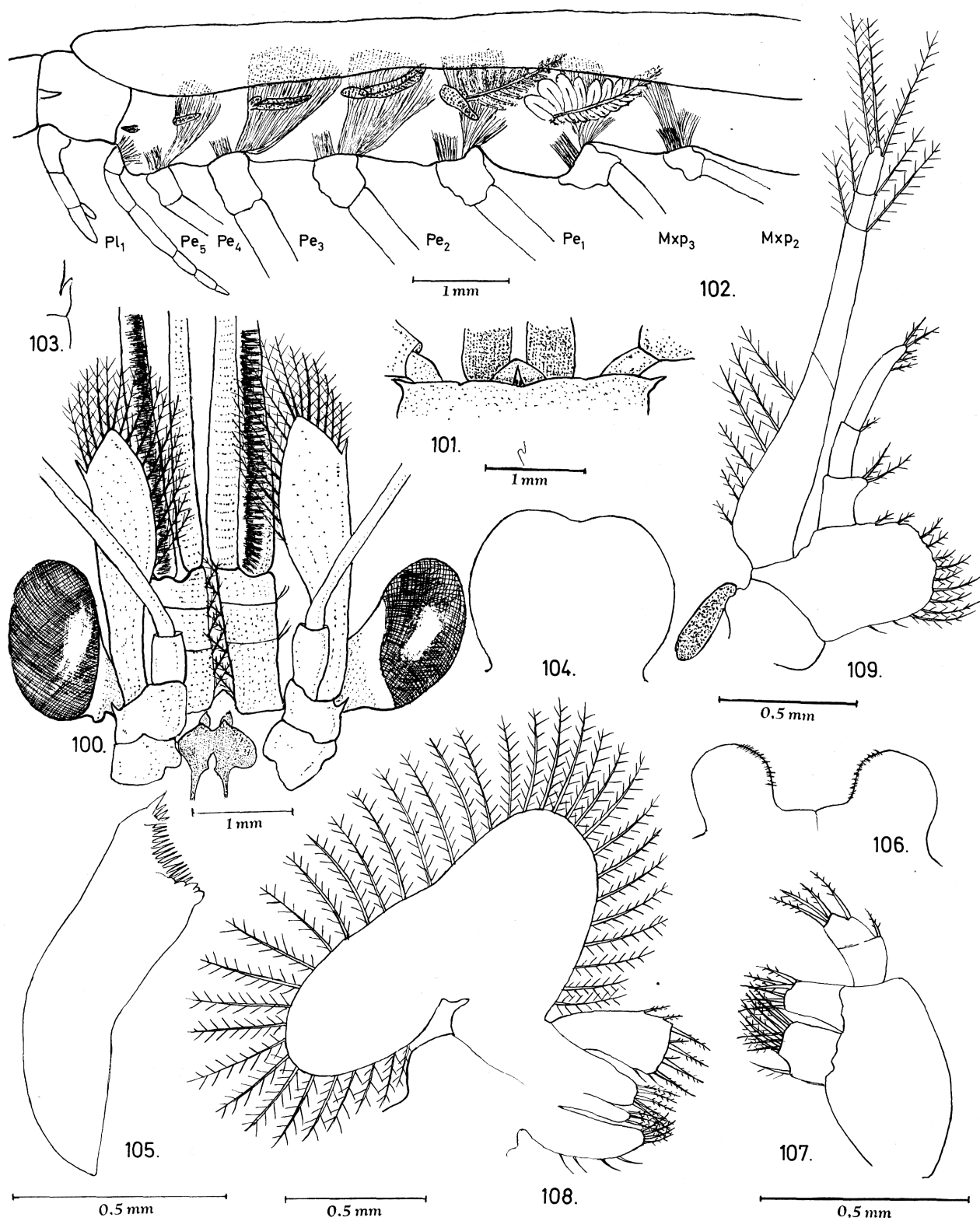
Figs. 95, 99-116.

Development.

Both thorax and abdomen have grown. The anterior dorsal organ and its anterior projecting spine have enlarged (Fig. 110). The fourth pereopod is nearly as large as the preceding ones and an unbranched fifth pereopod 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 pereopods. 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 $\frac{1}{4}$ mm to more than $\frac{1}{2}$ 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 $1\frac{1}{2}$ 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.

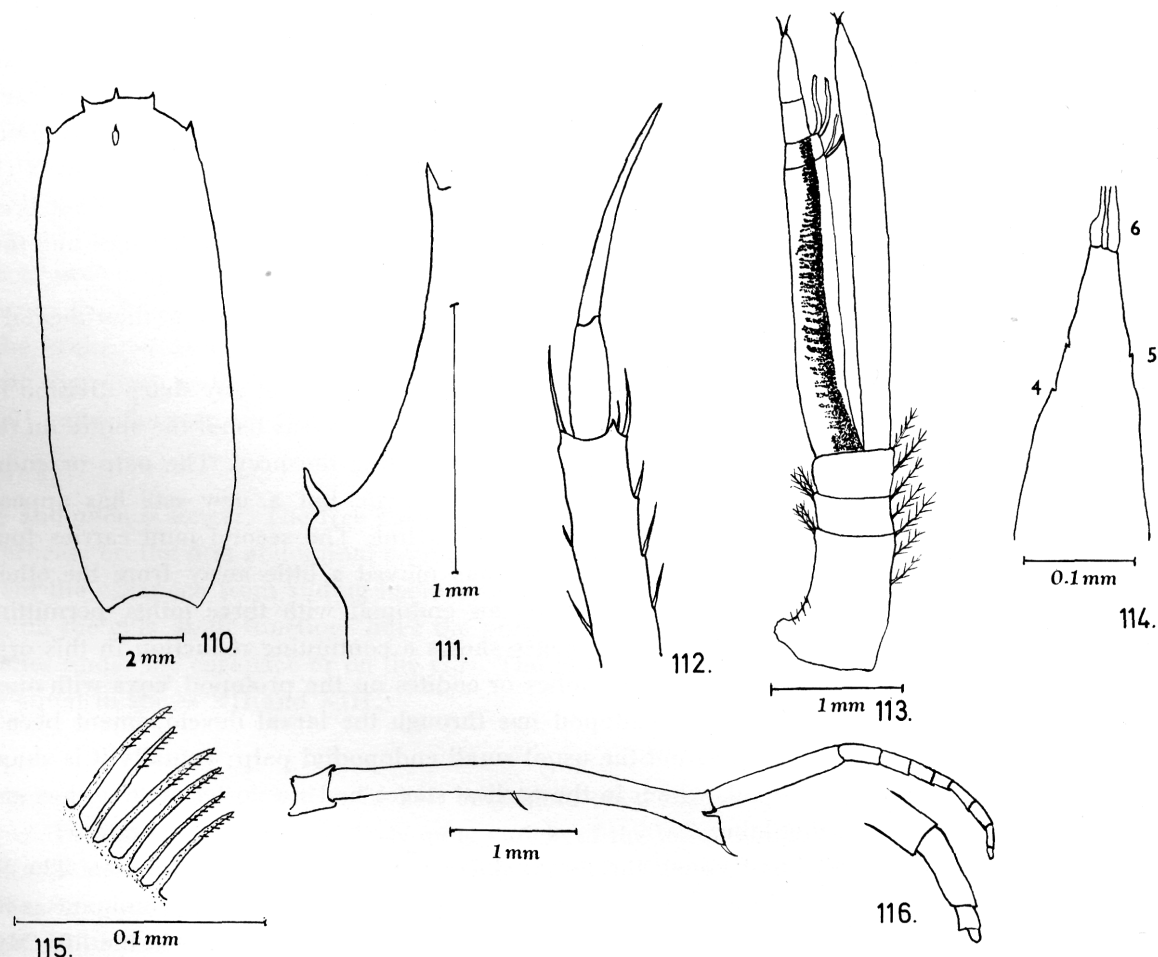
The first maxilla (Fig. 107) has developed a stout elliptical protopod without any sharp division between coxa and basale. The two endites remain and are placed close together, and as usual the spines on the basi-endite are the strongest and can be used as secondary teeth for cutting the prey. The palp 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 development 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 prominent 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 sickle-shaped 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 pereopod. — 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 pereopod 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.

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*".

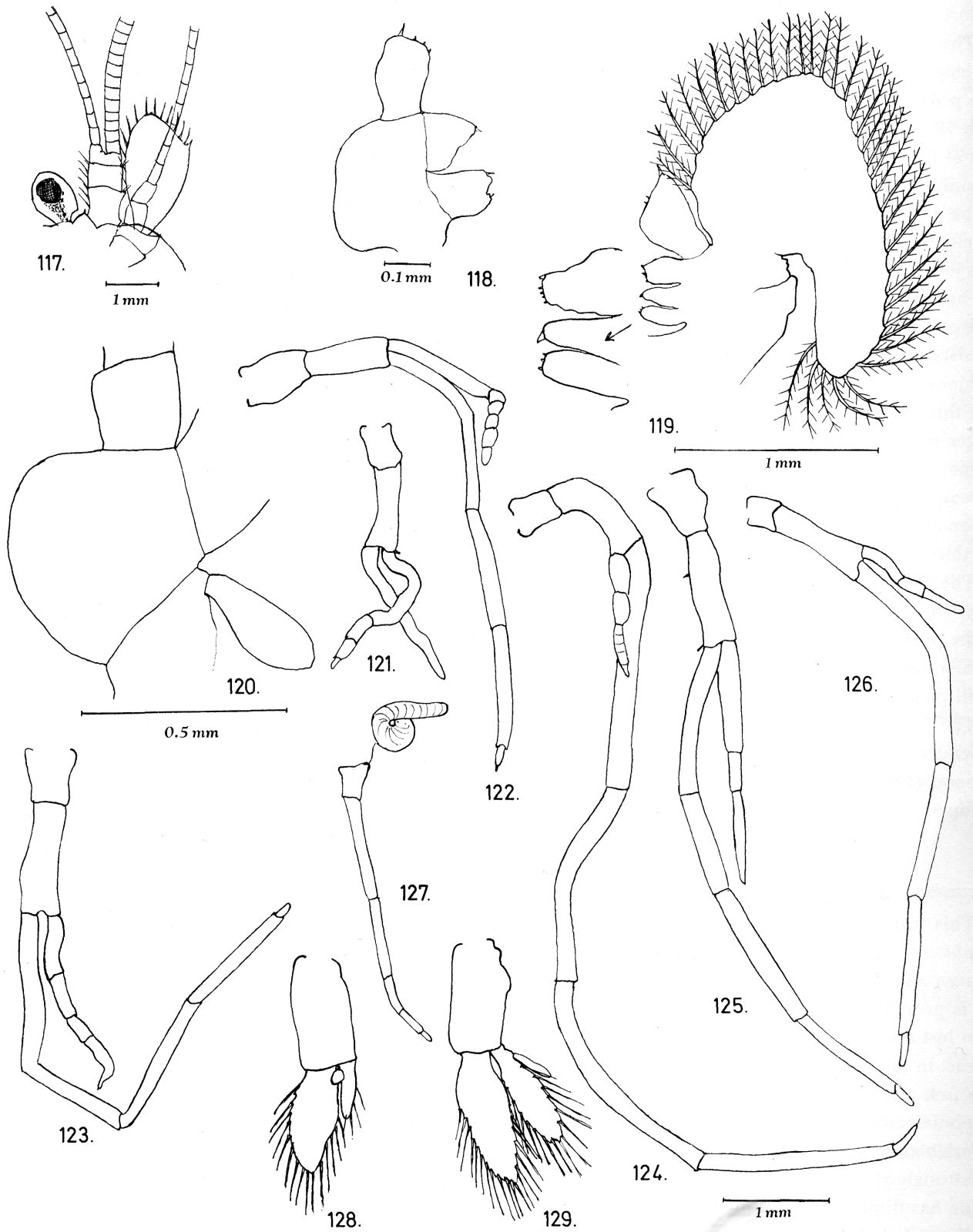
Due to the very poor state of preservation of the single larva of this stage in the material, the maxilla and part of the first maxillipede were the only mouth appendages present.

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 $\frac{1}{2}$ of the exopod to about $\frac{2}{3}$ 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 pereopods, 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 pereopod (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 pereopod (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 pereopod (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 pereopods. 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 pereopod (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 pereopod. 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 pereopods.

The fifth pereopod (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 pereopod; 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 pereopod 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 pereopod, 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 schmaler 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 pereopod 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.

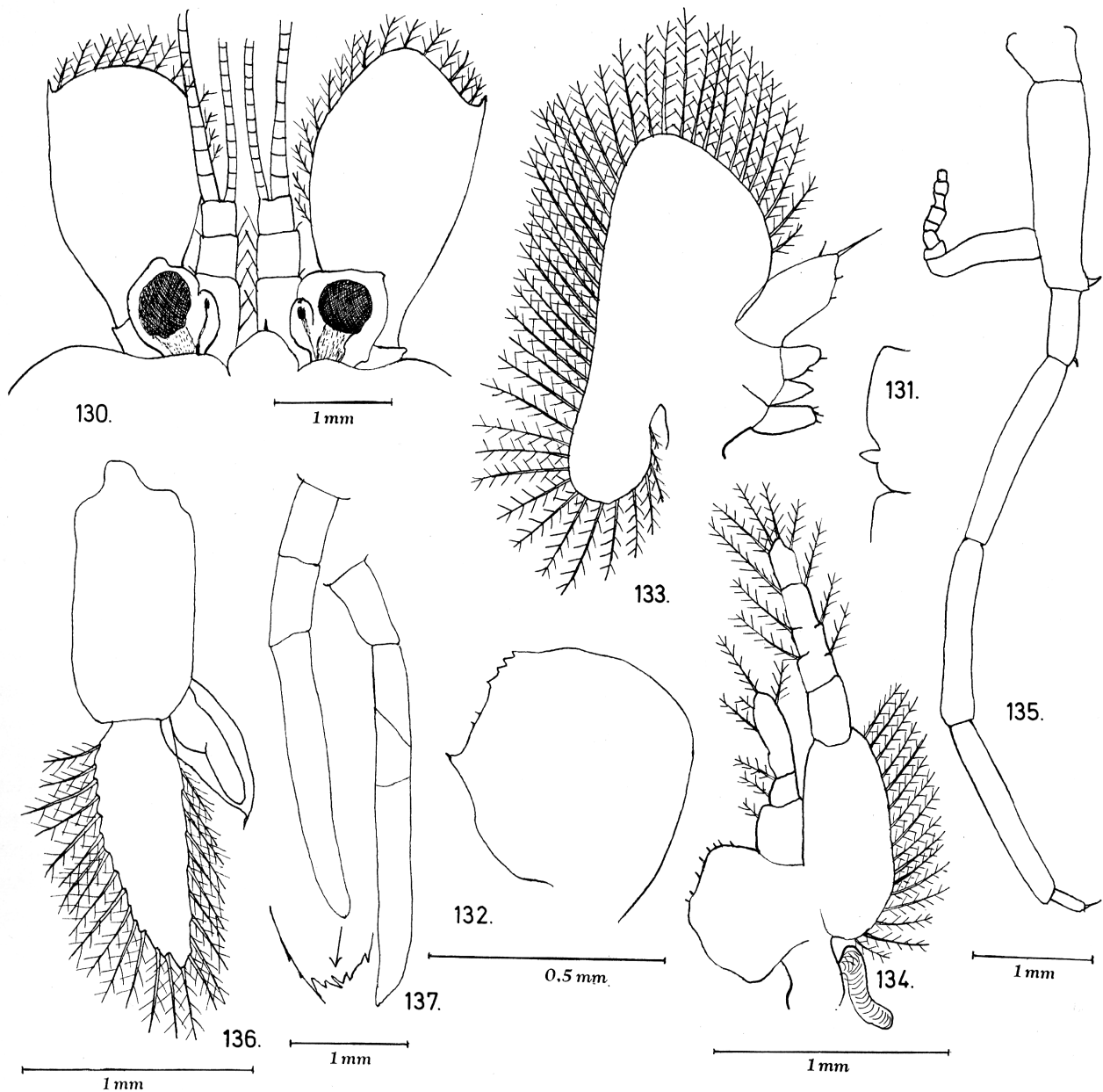
Localities.

“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 pereopods, except the first, are reduced further, especially their exopods, and only the second pereopod is larger, while the fifth pereopod 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 pereopod. — 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 Euphausiids 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 pereopod 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 pereopod (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 right 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—	} —	13 p. m., TYF	180	—	25. 8.1927.	3 —
			2700 m							
			depth							

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

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*.

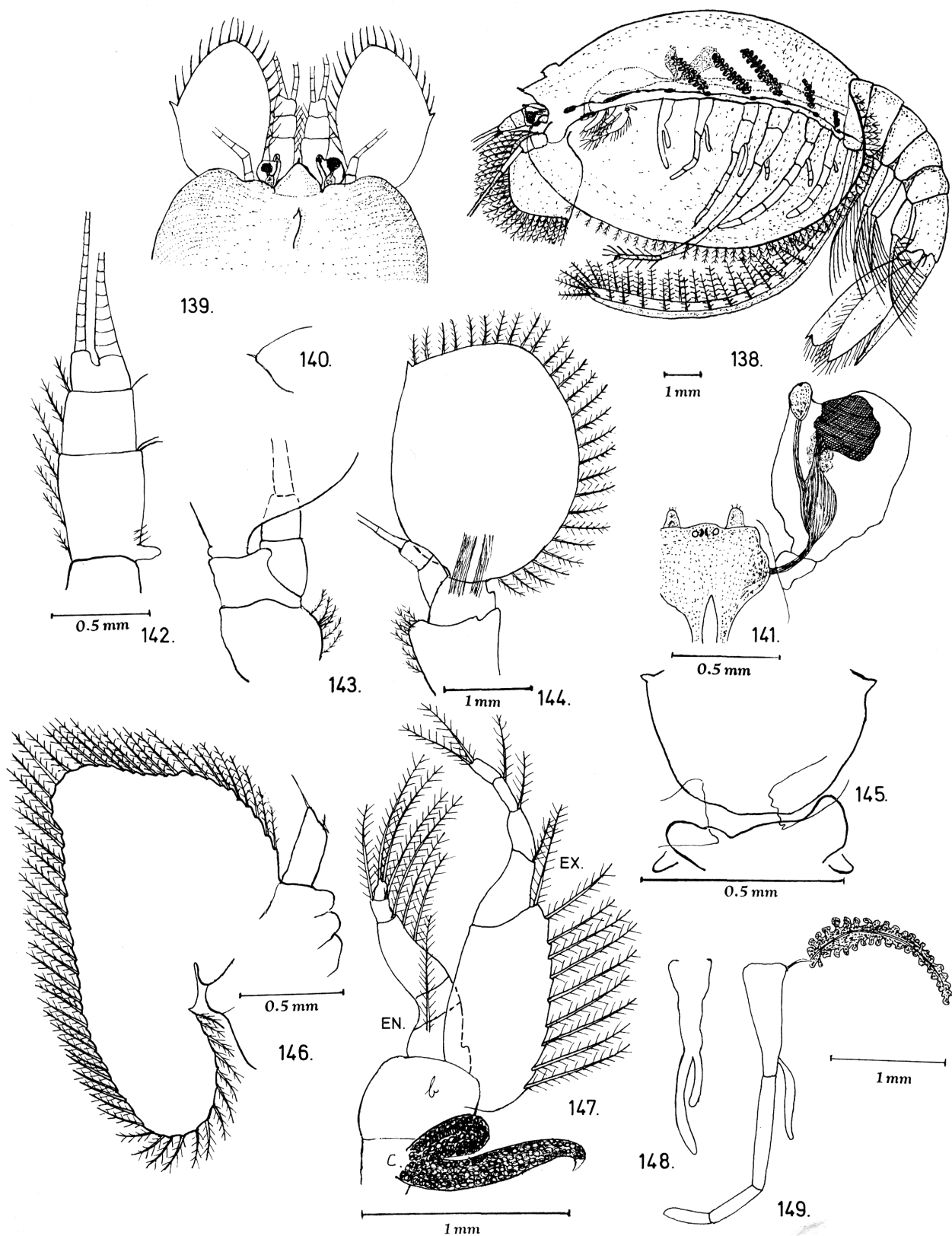
The reconstruction of the adult *Amphion* is rather difficult because, as GURNEY (1936) so rightly writes, "the thoracic region of these specimens is like a mass of torn and sodden tissue paper", or it reminds one of "*Beroe*" found in lumps in a plankton haul, only without the ciliated ribs, a picture 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.

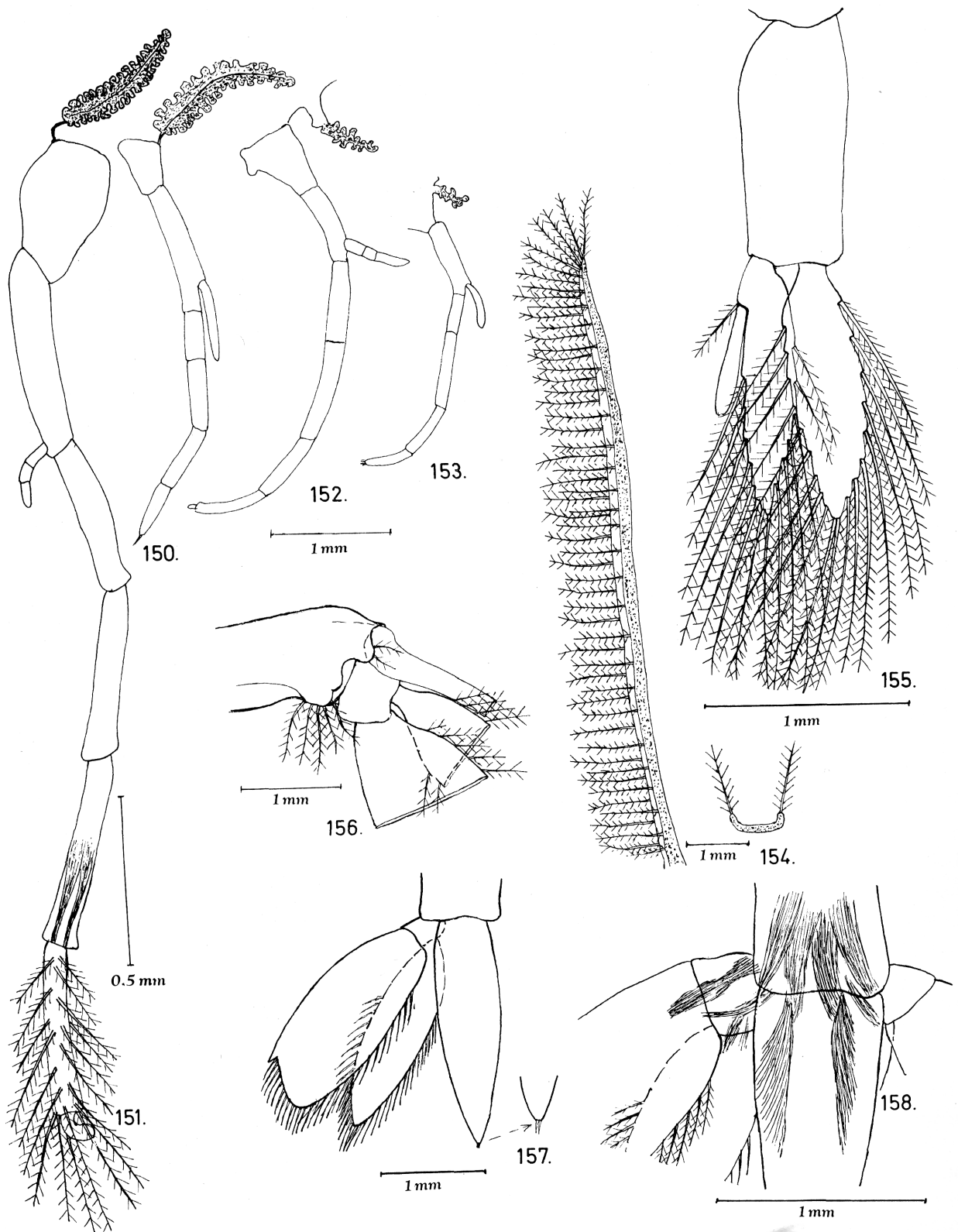
The carapace has finally grown to its full bell-shaped form. The orbital and antennal lobes of the carapace have enlarged. The marginal setae on the carapace have developed. The cuticle has become thinner on the carapace as well as on the abdomen. The muscles of the abdomen have strengthened and the 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.

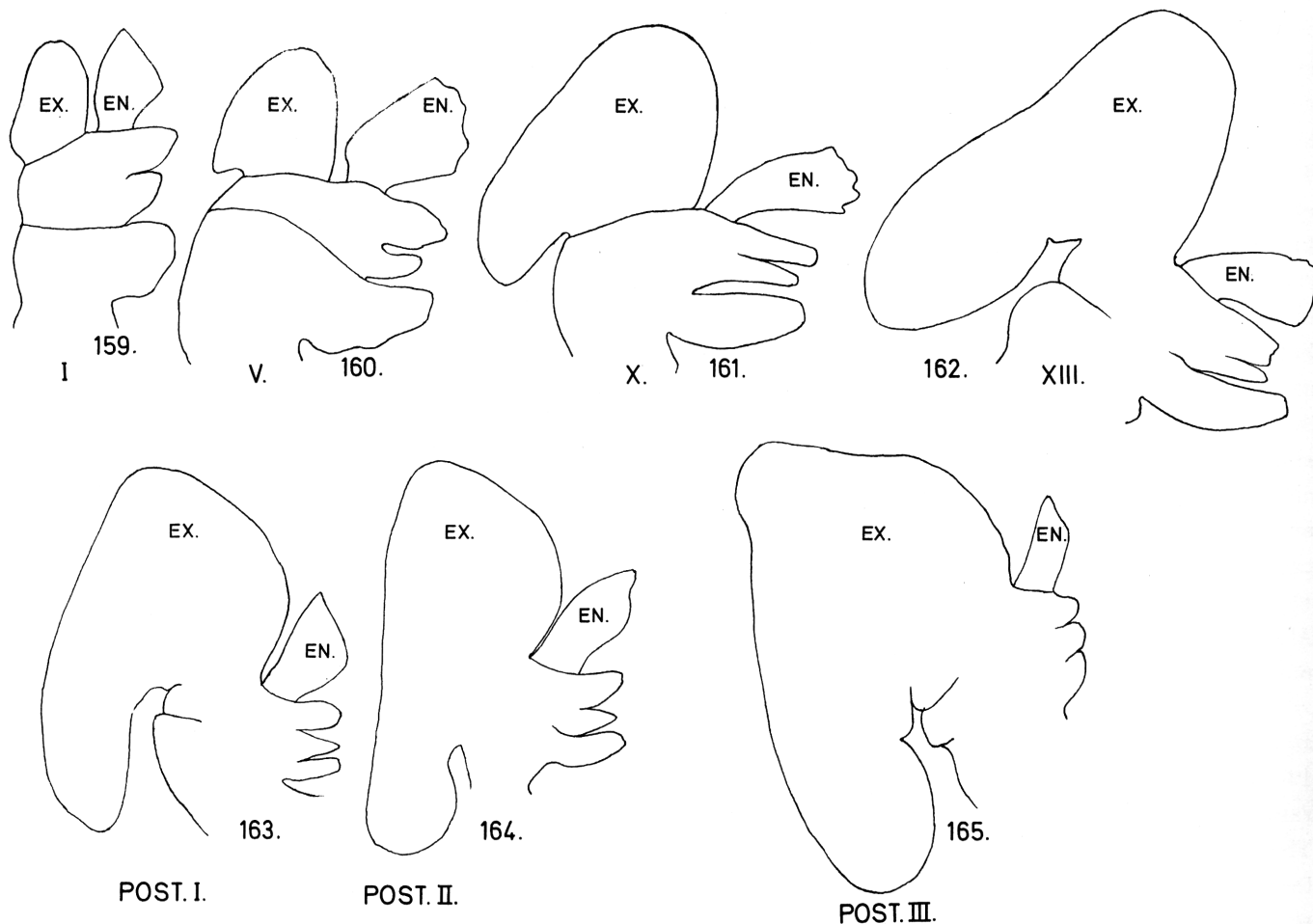
From Tables XII-XIV can be seen that the different larval stages are found throughout the year. We must therefore assume that spawning takes place throughout the year without any larger seasonal break.

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 copepodial 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).

I have not been able to find a natural explanation for the late final development of lenses in the nauplius eye in *Amphion*. Throughout the larval life the nauplius eye is without lenses and first in the adult (Figs. 141) a lens develops near each of the eye cups, and only at a distance from the sensory epithelium, which shows its inability to function. In this stage, in 2000–4000 m depth, the adults are living in absolute darkness. They have the stalked, lateral eyes with their luminescent organs, but why should there be lenses in a nauplius eye which is embedded in the brain tissues? Perhaps some glandular hormone function, of which we yet know so very little, is connected with it, or the lenses in the adult may have an atavistic explanation.

It is of interest to note the presence of the lateral process on the first abdominal segment. This is found in Penaeidea larvae and on the second abdominal segment on the Zoea in Brachyura but not found in Caridea before. It is now seen in *Amphion* from the first larval stage and continuously through the larval stages and at least to the second postlarva included. This must be considered a primitive character still remaining in this primitive Caridean shrimp. Here it can be noted that in a still unpublished paper, I have found the same abdominal process in another Caridea, *Chlorotocus crassicornis* (COSTA), Pandalidae. This is to my opinion also in many aspects a primitive Caridea. It may be more generally found in some Caridea, only having been overlooked. This has still to be investigated, in my Napoli investigation (HEEGAARD, 1963) I looked for the process on the investigated species, without finding it.

Only one *Amphion* species exists, *A. reynaudi* M.-EDW., for which *A. provocatoris* BATE is a synonym. Also *Amphionides valdiviae* ZIMMER is reduced to a synonym for *Amphion reynaudi*, being the postlarva and possibly the adult of this species.

The growth of the larvae appears to be very slow. We find here the largest number of larval stages in any known decapod species. The value of the growth factor has been discussed in an earlier paper (HEEGAARD, 1966). In Table I of the present paper it can be seen that in my *Amphion* investigations the growth factor ranges from 1.04 to 1.38, which shows firstly that it is extremely low, secondly that it varies considerably. The planktonic food for such small organisms is rather poor in the tropical parts of the oceans. We will therefore also find that the highest growth factor is from the first to the second stage where some yolk still remains from the egg. The growth factor from Promysis to Mysis may possibly still be a little larger, but this is unknown. After the yolk has been consumed the growth factor becomes extremely low for a long time, between 1.04 and 1.13, which may indicate great difficulties in nourishment for the larvae up to the Xth Mysis stage. From this stage the larva has developed enough pereopods to shape a proper catching basket, which immediately results in the growth factor jumping from 1.05 to 1.38 and remaining around this figure until the twelfth Mysis stage, which is the second last Mysis stage. In the twelfth Mysis stage internal transformations towards the adult have started to take place, and now it grows more in width, a character not considered in the estimation of figures of the growth factor, which is based on total length.

In the postlarva and from this to the adult no growth factor has been estimated because a proper measure of the adult or postlarva was impossible due to the very soft and partly torn thorax of these stages. However, if this factor could be determined on dry material, as it really should, it would show a very low figure again, first of all because the food is much scarcer at 3000 to 5000 m depth where the shrimp now lives than in the surface water layers where the larval stages were passed.

In recent years attention has been paid to the fact that a given instar or larval stage of a species can vary. McDONALD (1926, 1927) first called attention to this phenomenon in the Euphausiids and later FRASER (1937) clearly confirmed this variation for *Euphausia superba*, and reduced its true number of larval stages to about one third. The understanding of this problem has in recent time advanced further by showing that the number of larval stages of decapod Crustacea may vary within the same species under different living conditions (PROVENZANO a. o.). However, the factors involved have not yet been clarified. But going to the extreme this means that no definite description is valid for a larval stage because there is a certain range of variation within each instar. This is further understandable from the fact that within the Crustacea the eggs themselves in most cases show a rather surprising variation in diameter within the batch of one and the same female. This again results in much more yolk in the larger eggs and a far better start in life for the larvae hatched from these eggs compared with those hatched from smaller eggs. This advantage for some of the larvae, which

begins at the moment of hatching increases through their larval life as they are more vigorous and therefore catch more food and obtain a better nourishment, enabling them to reach a higher degree of development between the ecdyses. It must be borne in mind that crustacean larvae, like all other larvae, grow constantly, but that in the Crustacea this is not macroscopically visible due to the cuticle, which until it is shed prevents an increase in size. But mitotic divisions of the cells occur continually as in all other growing organisms. In the Crustacea however, the new cells remain in an embryonic state which means that their nuclei and protoplasm are kept nearly as dry material inactive and taking up very little space, so that they can find room inside the existing cuticle, similar to what is the case in a plant-bud. First during the ecdyses these new cells absorb water at the same time becoming activated, living cells.

These advantages for the larvae hatched from the largest eggs are among the more important factors for a quick and evenly accelerated growth throughout the larval development, what can be seen for *Amphion* from the figures in Table III-V. In the early stages only a 1 mm difference exists between the smallest and the largest larva, and this continues up to the fifth Mysis stage. However, one must remember that the number of larvae of these first stages is relatively low in the material, which makes the figures for these stages a little less valid than for the later stages. Personally I am convinced that an adequate number would not have widened the range much, but all the same the tendency is clear and cannot be denied. In the sixth and seventh Mysis stages we have a maximal variation of 2 mm, in stage VIII and IX of 3 mm. This variation now accelerates quickly, also because of the development of a better catching apparatus, so that in the last two Mysis stages, XII and XIII, the difference in length between the smallest and the largest larvae of the same stage in the different oceans ranges from 9-14 mm, which is more than 50% of the total length. The length remains nearly the same from stage XII to XIII, but this has already been explained by the fact that in this interval the growth is mainly in the width of the thorax, and not in the total length which is used for these growth figures.

Another point of interest is the two completely different catching apparatuses. The first is found in the surface form of the larva, the Mysis, in which a catching and grabbing trap is shaped by the pereopods and the two last maxillipedes. The second and differently built is found in the adult, which lives in depths between 2000 and 4000 m. Here the cuticle has become paper-thin as in many deepsea organisms and very little lime if any is encrusted in it. The reason for this is not absolutely clear, but it can be pointed out that the pH in the surface water of the ocean is about 8.2 but from about 1000 m and to the bottom this figure has fallen to about 7.8 or lower. We have in the ocean a balance between the carbonate and the bicarbonate ion and with decreasing pH the balance travels towards the bicarbonate ion so that we get more bicarbonate and less carbonate in the water. Because the Crustacea must use the carbonate ion for encrusting lime in the cuticle it means that animals living in deeper water layers have more difficulties and need more energy to build up the same calcareous cuticle which they were wearing in the surface layers, and this may be a reason why so many crustaceans from the abyssal zone have a thin cuticle with little lime in it. In the adult *Amphion* (Fig. 138) it can be seen that all the pleopods except the second, and the two last maxillipedes, have become thin-skinned strongly reduced limbs with very few muscle fibres, because these would have nothing to fasten to with the hardening of the external skeleton lost. Of limbs, the antenna, the mouth appendages, the second pereopod, the pleopods and the tailfan have got all the available calcium carbonate, thus the external skeleton becomes strong enough for the muscle attachment of the only functional limbs.

But apart from this, the trap which served the *Amphion* larva well in the surface water would be of no use if it still existed in the adult in the abyssal zone as so few organisms live here that the adult shrimp would not be able to catch sufficient food through such a simple trap system, as that used by the surface larva.

Instead we have seen that the adult has developed a strong luminescent organ of the secreting type with luciferin in the stalked lateral eyes. By placing it in the eye the light beam can be steered together with the eye in different directions. With the light turned on it must be able to attract smaller organisms with either eyes or light sensitive organs living in these water layers.

We must then imagine that *Amphion* stands in the water moving as little as possible with the light on, the bell-shaped carapace open and hanging down and the abdomen stretched horizontally out from it. When

Table III. *Amphion*. Atlantic Ocean. Numbers and length in mm of specimens of each larval stage, I-XIII.

mm	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Number	
XIII															5	33	29	22	14	15	14	5	3	0	2			142	
XII															4	23	24	13	12	18	12	6	3	3	2			117	
XI											10	42	76	71	42	6		1										248	
X							2	19	124	94	103	57	6	1														406	
IX						3	68	100	4																			175	
VIII							7	121	58	5																		191	
VII					5	63	19																					87	
VI		4	59	36																								99	
V			8	12																								20	
IV	4	14																										18	
III																												0	
II		9																										9	
I																												0	
Total...																													1512

Table IV. *Amphion*. Indian Ocean. Numbers and length in mm of specimens of each larval stage, I-XIII.

mm	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Number	
XIII															3	20	35	51	17	33	35	21	17	1				243	
XII															2	9	14	26	38	22	38	28	25	5	2	1	1	211	
XI																48	94	62	42	9	4	3						262	
X									9	125	153	108	75	6	2													478	
IX							102	122	18	4																		238	
VIII						21	129	64	4	2																		220	
VII					4	84	15	1																				104	
VI				108	21																							129	
V		1	34	12																								47	
IV	44	32																										76	
III	2																											2	
II	24	10																										34	
I	1																											1	
Total...																													2045

Table V. *Amphion*. Pacific Ocean. Numbers and length in mm of specimens of each larval stage, I-XIII.

mm	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Number	
XIII																	11	18	7	14	14	9	7	5	4	2	1	92	
XII																1	6	18	9	10	11	10	8	8	6	4	1	92	
XI																1	47	52	29	10	2							141	
X										6	43	42	64	54	3													212	
IX							34	46	2																			82	
VIII					5	61	14	1																				81	
VII				2	43	10																						55	
VI			46	17	1																							64	
V			12	8																								20	
IV		6	41																									47	
III		1	2																									3	
II	2	36																										38	
I	2																											2	
Total...																													929

the prey comes near to the "lantern", *Amphion* must be expected to slowly move itself into a favourable position, so that it is able with the large antennal plates — furnished with strong muscles — and the pleopods to produce a strong current running forwards-backwards up through the bell of the carapace, which current will suck the prey into the bell. The bell can then be closed with its own, although weak, muscles so that its marginal setae meet from each side. The resulting fissure can then further be closed medially by the long first pleopods, and at both ends by the antennal plates and the telson fan formed by uropods and telson plate. All these parts can through contractions in their strong musculature be bent in underneath the bell-shaped carapace so that no escape is possible for the prey. After that the long second pereopod with its fourth joint shaped as a lamp-brush can function like a piston within the bell and push the prey into the mouth. The hook-shaped fifth joint (Fig. 151), similar to the hooks given to many war-invalids who had lost an arm, is well fitted for pushing the last prey particles into the mouth. When the prey thus has been eaten *Amphion* can turn on the light again and prepare itself for another catch. A second function for the second pereopod must be as a cleaning-brushing organ which easily can reach everywhere among mouth appendages, thoracopods, gills and even through the pleopods.

SYSTEMATIC POSITION

It has been mentioned (pp. 8-9) that H. MILNE-EDWARDS (1832, 1837), BOAS (1879, 1880, 1883, 1939) and ORTMANN (1893) placed *Amphion* near *Phyllosoma*.

CLAUS (1876), KOEPEL (1902), and BALLS (1927) were of the opinion that *Amphion* belonged to the Sergestidae; CLAUS even that it was a species of *Acanthosoma*. KORSHELT & HEIDER (1892) and GURNEY (1924, 1936, 1942) referred it to the Caridea. In 1924 GURNEY noted a great similarity to the *Eretmocaris* larva which is usually placed in Lysmatidae, or as the genus *Lysmata* in Hippolytidae. Later (1936) he placed *Amphion* and *Amphionides* in their own family under the Caridea, and in 1942 *Amphion* was without argumentation claimed to be the larval form of *Amphionides*.

BATE (1888) established two species, *Amphion reynaudi* M.-EDW. from the Pacific with a rostral but without a post-rostral spine, and *A. provocatoris* BATE from the Atlantic without rostral but with post-rostral spine. This was rejected by ORTMANN (1893) and GURNEY (1936), and it is also rejected in the present paper, because all larvae, whether from the Pacific, the Indian or the Atlantic Ocean, have both rostral and post-rostral spine, the latter in younger larvae looking like an anterior dorsal organ. All hitherto known *Amphion* larvae belong therefore to one and the same species which by priority must be *Amphion reynaudi* M.-EDW.

Concerning the systematic placement to or near the *Phyllosoma* larvae can be said the following:

There are very strong superficial similarities between *Amphion* and the *Phyllosoma*, but I do not consider them to be of phylogenetic or systematic significance. Both have — it is true — a flattened carapace and thorax with a flattened, branched hepatopancreas, but whereas this organ is simple-branched in *Phyllosoma*, in *Amphion* it is divided into different sections, one of which is a pair of backwards-running tubes without secondary branches, but with many short lobal outgrowths. Further, the endopod of the thoracopods is four-jointed or, if the claw is included, five-jointed, in both *Amphion* and *Phyllosoma*, and five-jointed in the adult of both when functional. The gills, however, are pleurobranchiae in *Amphion*, but podobranchiae in *Phyllosoma*.

Considering the thoracopods, *Cerataspides longiremis* (DOHRN) of the Penaeidae could also be claimed a near relative. The thoracopods here, apart from their locomotory exopod, are also developed into a trap organ for catching plankton. But *Amphion* can belong neither to Reptantia like *PHYLLOSOMA*, nor to Penaeidae like *Cerataspides*. The shaping of thoracopods in much the same way in these three decapods is caused by almost identical living conditions: all are planktonic, feeding on smaller planktonic organisms in the upper layers of the open ocean, and all three have independently acquired nearly the same catching methods, which must be parallel running analogies, but no homology can be found in them. I consider them therefore of no phylogenetic bearing.

Phyllosoma has a typical flattened reptant abdomen, but both *Cerataspides* and *Amphion* have the typical natant, compressed abdomen. The antennae in *Amphion* are not reptant but caridean in development, and all mouth appendages are quite different from those of *Phyllosoma*. The two long lobes on the labium are placed close together in *Phyllosoma*, a reptant character, but in *Amphion* they are short and placed far apart. The first maxilla is with its slim, palp-shaped endopod of the reptant type in *Phyllosoma*, but in *Amphion*, as long as it is in function, which means in the surface-living stages, the endopod develops into a secondary, stout, masticatory process with stiff spines. Its later disappearance in the abyssal form is a secondary reduction without phylogenetic value. In the second maxilla of *Phyllosoma* the endites are fused into a single, undivided plate which is further enlarged in the adult *Palinurus*; the endopod is absent (small in *Palinurus*) and the exopod has the normal anterior and posterior processes of the scaphognath. *Amphion*, however, has three

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separate endites, one coxa endite and two basi-endites, but not the usual four endites. The endopod is shaped and functions as a fourth endite. In young stages the exopod has only the anterior process. The posterior process develops first during the larval stages, a fact which also may have some bearing on *Amphion's* systematic position.

In the adult *Amphion* the three endites are still present but much reduced, the endopod is diminishing through the whole development and the exopod is enlarging. Thus, the developmental trends are just opposite of those in Palinuridae.

The first maxillipede in *Phyllosoma* is a small, rudimentary organ without an exopod, but still with a mastigobranchia. First in the adult *Palinurus* does it reach normal development. In *Amphion* it is the only functional maxillipede, with both exopod and endopod, gnathobase on the basale, and on the first endopodial joint, and a mastigobranchia from coxa. In *Amphion* the two following maxillipedes are developed as ordinary thoracopods and with an open space to the first maxillipede. Finally they are reduced together with the thoracopods in the adult. In *Phyllosoma* the second maxillipede is the functioning maxillipede and has very short and non-functional swimmerets.

An appendix interna is present, it is true as remarked by BOAS (1939, p. 26), on the pleopods in both *Amphion*, *Polycheles*, *Homarus* and in many Reptantia, but it occurs also in some Caridae (*Pasiphaea*) and its presence in Leptostraca, Euphausiacea, and Stomatopoda shows that most likely it must be considered a primitive feature among the Malacostraca, therefore it can have no systematic bearing for Reptantia. BOAS (1939, p. 24) finds a phylogenetic point in that in the thoracopods of both *Phyllosoma* and *Amphion* the first joint is short, the second long, while the third, fourth and fifth joints are equally long. This, however, can have no phylogenetic bearing. It is necessary for the shrimp to be able to displace the most flexible and more distal part of the limb a little from the thorax, so that it can be turned dorsally along the side of the thorax for shaping the semicircular part of the catching trap. To give the limb strength, the first joint must be shortened. The same procedure is adapted for shaping a long walking limb in both Reptantia and Caridea.

The arguments in the literature for *Amphion* being a reptantian and the objections to these arguments can be summarized as follows: 1. *Phyllosoma* appendages and hepatopancreas — but the former are found in other decapods and both have no systematic bearing. 2. A diminutive rostrum — but this is also found in some Caridea. 3. The gill formula — but this does not appear more closely related to *Macrura* than to Caridea, on the contrary, most reptants have at an early stage a multiplication of the pleurobranchia, *Amphion* has only one in each segment. 4. The late development of the pleopods — but this is also seen in other Caridea, and *Amphion* has no need for pleopods as long as it is a true plankton organism. 5. Appendix interna on the pleopods — but this is found also outside the decapods.

All these points should be more than sufficient for showing that there is no closer genetic relationship between *Phyllosoma* and *Amphion*. The points in which they resemble each other are only superficial, of a biological character, and acquired for serving the same mode of life in the same biotope, but do not indicate a closer genetic relationship. The mouth appendages especially show the great difference between the two forms. One is a reptant decapod, the other is not.

The second assumption advocated by CLAUS (1876), KOEPEL (1902) and BALLS (1927) that *Amphion* is a Sergestid must also be rejected.

The Sergestidae belong to the Penaeidea and like the rest of this group hatch as a Nauplius larva, after which follows a Protozoa, both with the first antenna as the locomotory organ.

When I in this paper, as in others, reserve the name *Zoea* for *Brachyura* and therefore use *Mysis* for all known *Amphion* larvae, it does not indicate that the earlier *Amphion* is not in a development which by some authors is called *Zoea*. — If *Amphion* were a Sergestid or closely related and thus included in the Penaeidae, we should expect the Protozoan first antenna in *Amphion*, but instead we find a first antenna as that of the non-Penaeid, decapod Crustacea. Further, the larva described in this paper as the first *Mysis* is by the character of its first antenna, first and second maxilla, telson and other organs definitely the first free stage after the hatching stage, and if it were related to the Sergestidae it should therefore show at least some Protozoan characters, which it does not. It is at present an open question whether some of the Penaeids have lost the

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Nauplius stages and hatch as Protozoa, but if this is the case, they do hatch as Protozoa with the typical first and second antenna as locomotory organs and never in shape of a Zoea or Mysis. These reasons alone are sufficient to prove that *Amphion* cannot be included among the Sergestidae or any other of the Penaeidae.

Finally, KORSHELT & HEIDER (1892, pp. 461–62) and GURNEY (1924, 1936, 1942) referred *Amphion* to, the Caridea, on the grounds that it was the only remaining group to which *Amphion* could belong (GURNEY, 1924, p. 105). On this I agree. *Amphion* has most of the typical characters of a Caridean larva.

Each time, however, GURNEY placed it differently within the Caridea. In 1924, p. 105, he thinks "it has a considerable degree of similarity to the *Eretmocarid* larva". This seems based mainly on the thoracopods, which are one of the most inconstant characters in decapod larvae, in *Eretmocarid* developed partly as a floating organ, partly as a trapping organ, as in *Amphion* and *Cerataspid*. Unfortunately, the mouth appendages of *Eretmocarid* are not described (GURNEY-LEBOUR, 1944, pp. 124–128), but both first and second maxillipedes are functioning as mouth appendages, while in *Amphion* only the first maxillipede has this function, even in the adult. It is also to be noted that *Eretmocarid* has no supra-orbital spines, but these are present in *Amphion*. Both antennae in *Eretmocarid* are quite different from those of *Amphion*. Thus, with our present knowledge we must leave that relationship out of consideration.

In 1936 and 1942 GURNEY placed *Amphion* as the larva of *Amphionides*. In 1936 as a possibility, in 1942 as a certainty. It is interesting to note that both GURNEY and ZIMMER, judging by their descriptions, have had the two stages here described as Postlarva I and II, but considered them as females of *Amphionides*, and that GURNEY without using the proofs at his disposal still felt that *Amphionides* was the adult of *Amphion*.

The next point is to see if there are any characters in *Amphion* which would indicate its placement in the Caridea.

The protopod of the second maxilla has only three endites, one on the coxa and two on the basale, a reduction from the normal 2+2. This reduction is compensated by the characteristic development of a fourth functional endite on the endopod, and of the masticatory lobes on the basale and first endopodial joint of the first maxillipede. Three true endites on the second maxilla are not common in the Reptantia, but are known from different Caridea: most Pandalidae, *Athanas nitescens*, *Leptochela carinata*, *Acanthephyra* (Oplophoridae), and in some other Caridea.

Further, the scaphognath of the second maxilla has a more detailed development than usual (Figs. 159–165). In the younger stages it points forward, and the normally in decapods developed posterior lobe seems missing (Fig. 159). In the fifth Mysis a posterior lobe starts to develop (Fig. 160). In the tenth Mysis it has reached a larger size (Fig. 161) but first in Mysis XIII, which is the last stage in the surface life, is it fully developed into a normal scaphognath. The exopod begins more like an exopod on a pereopod and first later are the two lobes of the typical scaphognath developed. Finally in the abyssal postlarva and adult *Amphion* the anterior lobe of the scaphognath reaches an overwhelming dominance (Figs. 163–165), which must enable it to produce a strong water current inside the carapace-bell. This first part of the development up to Mysis XIII is found also in all the Pandalidae of which the younger larval stages are known, as well as in *Processa bermudensis* (Processidae), in *Mesocaris* sp. (Pontonidae) and in *Acanthephyra* (?) sp. (GURNEY, 1924, Fig. 40d) (Oplophoridae) and partly in *Phyllosoma* of the Reptantia. In *Amphion* the last development of a dominating anterior lobe in the scaphognath must be considered as a special development caused by the life in its abyssal stages.

As these first-described characters are found in all known younger larvae of Pandalidae it could be tempting to assume a closer relation between *Amphion* and the Pandalidae, but other characters speak against a closer relation, all Pandalids have a well-developed rostrum, but *Amphion* only an extremely diminutive one, and *Amphion* further develops a rostral plate in the post-larval and adult stages.

Also from the Oplophoridae *Amphion* shows several differences, e.g. the Oplophoridae have both pleurobranchiae and arthrobranchiae, but *Amphion* has only a single line of pleurobranchiae.

In the Pasiphaeidae the rostrum is small or lacking, endites on the second maxilla are vestigial, and exopods are present on all pereopods, all this agrees with *Amphion*, but in Pasiphaeidae the basale of the first maxillipede is reduced, which is not the case in *Amphion* where it is very large in the surface form, and

in the adult — although partly reduced — still larger than general in the decapods. Further, the two first pereopods are enlarged in Pasiphaeids. In *Amphion* only the second pereopod is enormously enlarged, but more important is the presence in *Amphion* of a rostral plate which in Natantia only is known in the Penaeids. Finally, in *Amphion* only the first maxillipede is functioning as a maxillipede, but not the two following maxillipedes. Still more important is the presence of a large open space between the first and the second maxillipede so that the two last maxillipedes also to judge from their placement, still belong to the thoracopods. These points are very important because we have to go back right to the Euphausids to find an analogous structure of the maxillipedes, and this structure is by all investigators considered a primary primitive character.

Based on the above-mentioned considerations I place *Amphion* in its own family Amphionidae and as the only family within the sub-tribe Amphionidea under the Caridea (if not forming its own tribe), and consider it as possibly the most primitive of the known Caridea although some of its reductions are of a secondary character. It is primitive especially on account of its maxillipedes, rostral plate, and single line of pleurobranchiae.

TRIBE CARIDEA

Sub-Tribe Amphionidea

Caridea with only first pair of maxillipedes functioning as maxillipedes. The following two pairs of maxillipedes are developed like the following thoracopods. Exopods are present on all maxillipedes and pereopods.

Pleura of second abdominal somit not overlapping those in front, and antennae without stylocerite.

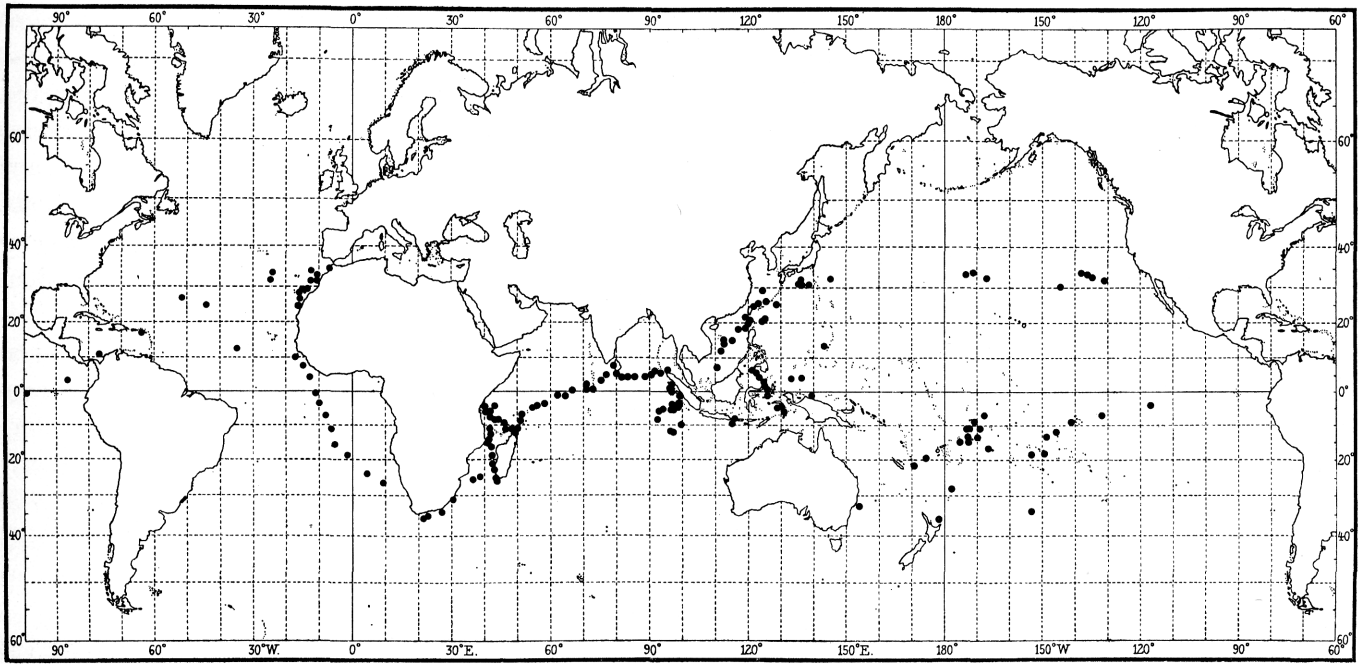
Family Amphionidae

Rostrum diminutive, rostral plate and nauplius eye present: second maxilla in larva first with exopod and endopod parallel with longitudinal axis of the protopod, later the endopodial axis turns 90° to the two others, and in the adult it returns to its original position: endites on same limb much reduced. Appendix interna on pleopods. Single line of pleurobranchiae on third maxillipede to fourth pereopod. Fifth pereopod missing in adult.

Genus *Amphion*.

Carapace in adult swollen, much enlarged, with anterior dorsal organ. Eye large and with luminescent organ, mandible reduced without molar part in adult. Limbs reduced, except second pereopod, pleopods large. First pleopod developed into a special feeding organ in adult, all other pleopods with appendix interna also the first pleopod before its transformation.

Only one species is known, *Amphion reynaudi* H. MILNE-EDW.



Map I. All "Dana" localities with *Amphion reynaudi*.

GEOGRAPHICAL AND VERTICAL DISTRIBUTION

Maps I-II. Tables VI-XIV.

In its geographical distribution *Amphion* is a typical tropical and subtropical form. It is found in all oceans between 36° North and 36° South. These are the boundaries for the "Dana" material as shown on Map. I. The "Discovery" Expedition had *Amphion* material only from the Atlantic, and the limits for the catches were 33° North and South.

Tables VI-VIII show the average number of catches of *Amphion* larvae from the different depths. With wire lengths of 600 m or less the gear has only been down about one third of the length of the wire. With wire lengths of 2000 m or more the gear has been hauled in depths about half the length of the wire.

Table VI. Atlantic Ocean. Number of *Amphion* surface stages I-XIII by depth zones and larval stages. Numbers caught and numbers converted to S-200 in 120 minutes.

Wire in m	surf.	50	100	200	300	600	1000	2000	3000	4000	5000	Total
Total number caught on 28 stations.....	10	1184	273	7	34	25	13	13	2	7	5	1573
Total converted.....	3840	1236	406	14	37	28	22	23	3	18	8	5635
Average conv. no. in % of total.....	68.14	21.93	7.20	0.25	0.66	0.50	0.39	0.41	0.05	0.32	0.14	99.99
Tot. conv. per stat. nearest full no.	137	44	15	1	1	1	1	1	0	1	0	202
Average conv. no. in % of tot. per stat.	67.82	21.78	7.43	0.5	0.5	0.5	0.5	0.5	0	0.5	0	100.03

Larval stage	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	Total
Number of measurable larvae..	0	9	0	18	20	99	87	191	175	406	248	117	142	1512
Number converted.....	0	11	0	405	407	452	92	205	577	1200	255	126	153	3883
Percentage caught.....	0	0.60	0	1.19	1.32	6.55	5.75	12.63	11.57	26.85	16.4	7.74	9.39	99.99
Percentage converted.....	0	0.46	0	10.43	10.48	11.64	2.37	5.28	14.86	30.9	6.57	3.24	3.94	100.57

Table VII. Indian Ocean. Number of *Amphion* surface stages I–XIII by depth zones and larval stages. Numbers caught and numbers converted to S-200 in 120 minutes.

Wire in m	surf.	50	100	200	300	600	1000	2000	3000	4000	5000	Total
Total number caught on 79 stations.....	16	1003	699	262	184	91	2	3	8	6	0	2441
Total converted.....	6144	1574	1066	315	245	138	5	6	16	13	0	9522
Average conv. no. in % of total.....	64.78	16.59	10.85	3.32	2.58	1.45	0.05	0.06	0.17	0.14	0	99.99
Total conv. per stat. nearest full no.	78	20	13	4	3	2	0	0	0	0	0	120
Average conv. no. in % of tot. per stat.	65.00	16.67	10.83	3.33	2.50	1.66						99.99

Larval stage	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	Total
Number of measurable larvae..	1	34	2	76	47	129	104	220	238	478	262	211	243	2045
Total converted.....	2	1205	2	1638	64	961	151	706	362	1862	962	697	364	8976
Percentage caught.....	0.05	1.66	0.10	3.72	2.30	6.31	5.09	10.75	11.64	23.37	12.81	10.32	11.88	100.00
Percentage converted.....	0.02	13.47	0.02	18.30	0.72	10.74	1.68	7.82	3.99	20.74	10.74	7.72	4.01	99.97

Table VIII. Pacific Ocean. Number of *Amphion* surface stages I–XIII by depth zones and larval stages. Numbers caught and numbers converted to S-200 in 120 minutes.

Wire in m	surf.	50	100	200	300	600	1000	2000	3000	4000	5000	Total
Total number caught on 46 stations ¹	2	526	261	10	33	17	5	7	6	3	1	871
Total converted.....	768	1895	744	24	112	44	21	15	15	9	2	3649
Average conv. no. in % of total.....	21.09	52.05	20.43	0.44	3.08	1.21	0.58	0.41	0.41	0.25	0.05	100.00
Tot. conv. per stat. nearest full no.	17	41	16	0	2	1	0	0	0	0	0	77
Average conv. no. in % of tot. per stat.	22.08	53.25	20.78	0	2.60	1.30						100.01

Larval stage	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	Total
Number of measurable larvae..	2	38	3	47	20	64	55	81	82	212	141	92	92	929
Number converted.....	9	87	400	167	65	271	191	272	322	1080	506	348	325	4043
Percentage caught.....	0.22	4.09	0.32	5.06	2.15	6.89	5.92	8.72	8.83	22.82	15.18	9.90	9.90	100.00
Percentage converted.....	0.22	2.16	19.91	4.14	1.61	6.72	4.73	6.74	7.78	26.77	12.54	8.62	8.05	99.99

¹ Samples from commercial vessels St. 4760–4820 not considered (see text).

From the "Discovery" material GURNEY (1936, p. 396) concludes "The figures do not prove anything, but suggest that *Amphion* may be more common between 200 and 500 m". The "Dana" material shows for all three oceans that *Amphion* in its Mysis stages — which were the stages GURNEY was referring to in the above citation — is a surface form occurring from the very surface and down to about 30 m depth. Only here must be taken into consideration that most of the "Dana" catches took place during evening and night.

The figures show that in the "Dana" material from the Atlantic Ocean 93% of the total converted number were caught in these upper layers, for the Pacific Ocean the figure is 96% and for the Indian Ocean 92.5%. Already in the hauls with 200 m wire, i. e. a gear working at about 60 m of depth, the numbers have decreased considerably to about 0–3% and these percentages are found down to a depth of 600 m. Below this depth the catch figures are still much lower, and all catches from these greater depths may have been taken in the net on its way up. Finally, Table IX includes all the hauls from stations with catches of *Amphion* with a wire length of 4000 m or more. This table shows that in the cases where specimens of *Amphion* were present in the net when it came on deck these may have been caught during the hauling up of the net when it passed through the upper water layers, as in all such cases there have been rather large numbers of *Amphion* taken in hauls with 50 and 100 m wire on the same station where the deep water hauls were made and at the same time.

Table IX. Numbers of larvae *Mysis* I–XIII caught in hauls from all depths on stations on which *Amphion* was caught with 4000 m wire or more. The first series in each column indicates the number caught, the second numbers converted to S-200 in 120 min. 0 indicates no catch of *Amphion* in that haul, and open spaces that no haul was taken with that length of wire.

Stat. no.	surface	Wire length m												
		50	100	200	300	600	1000	1500	2000	2500	3000	4000	5000	
3561....	0 0	1 4	6 24	0 0	0 0	0 0	0 0		0 0		0 0	2 8	0 0	Pacific
3676....	0 0	0 0	0 0	0 0	0 0	0 0	0 0		0 0		0 0	0 0	1 2	—
3917....	0 0	33 66	17 34		4 8	6 12	0 0		2 4		3 6	4 8	0 0	Indian
3920....	0 0	20 40	16 32		2 4	0 0	1 4		0 0	1 3	0 0	2 5	0 0	—
3998....	0 0	215 215	158 158		1 1	3 3	1 2	1 1	1 2		0 0	4 8	3 6	Atlantic
4000....	0 0	142 142	1 1		3 3	2 2	1 2		1 2		0 0	1 2	1 2	—
4003....	0 0	0 0	0 0		1 1	0 0	0 0		0 0		0 0	1 2	0 0	—
4017....	0 0	33 66	18 36		1 1	2 4	2 4	0 0	0 0		0 0	0 0	2 1	—
4019....	0 0	19 19	6 6		1 1	1 1	0 0		0 0		1 1	1 2	0 0	—
4180....	0 0	0 0	0 0		0 0	0 0	0 0		0 0		0 0	1 4	0 0	—

The "Dana" catches show a different picture than that suggested by GURNEY for depths between 200 and 500 m. However, it must be remembered, that nearly all "Dana" stations have been taken in late evenings or during night when the shrimp larvae may have taken part in the vertical night migration towards the surface, as known for many plankton organisms. On the other hand my own experience indicates that nocturnal migrations are not so common among planktonic organisms as one may gather from most text-books on the subject. However, also most of GURNEY's material was taken at night, only 10 out of 30 stations were taken at daytime, the remaining ones from late evening or night. But as the "Dana" material consists of not less than 5108 specimens of *Amphion* in Mysis stages, against only 97 specimens in GURNEY's material, I feel justified in concluding that at least at night *Amphion* is living in the uppermost surface layers down to about 30 m depth.

Where *Amphion* occurs at daytime is still unknown, and neither GURNEY nor the present material gives any clear answer. It can only be suggested that during daytime *Amphion* will be found in about the same water layers, except for the first five to six meters from the surface.

Figures showing the abundance of *Amphion* in the different oceans have been calculated and are presented in Table X, where we have the figures converted to the same duration of hauls and the same diameter of nets, i. e., to 120 minutes haul with a net with a 2 m opening, for the three oceans. The figures are given for different depths and as average number of specimens per hauls from stations on which *Amphion* was noted. If we again consider only hauls up to 100 m wire, which as has been shown includes 85% to 92% of the total number of hauls, it appears that in the Atlantic in these upper water layers were caught 65.33 specimens per converted haul. For the Indian Ocean this figure is 37 and for the Pacific 24.67. These figures show that

Table X. *Amphion* larvae (stages I–XIII). Average numbers per haul converted to S-200 and 120 minutes caught by the "Dana" expeditions in different depths.

Ocean	Wire length m											Total
	surface	50	100	200	300	600	1000	2000	3000	4000	5000	
Atlantic	137	44	15	1	1	1	1	1	0	1	0	202
Indian	78	20	13	4	3	2	0	0	0	0	0	120
Pacific	17	41	16	0	2	1	0	0	0	0	0	77
Total	232	105	44	5	6	4	1	1	0	1	0	399
Average	77.33	35.0	14.66	1.66	2.0	1.33	0.33	0.33	0	0.33	0	132.97
Total...												12.09

Table XI. Total number of *Amphion* Mysis stages caught and measured, both converted to S-200 in 120 minutes.

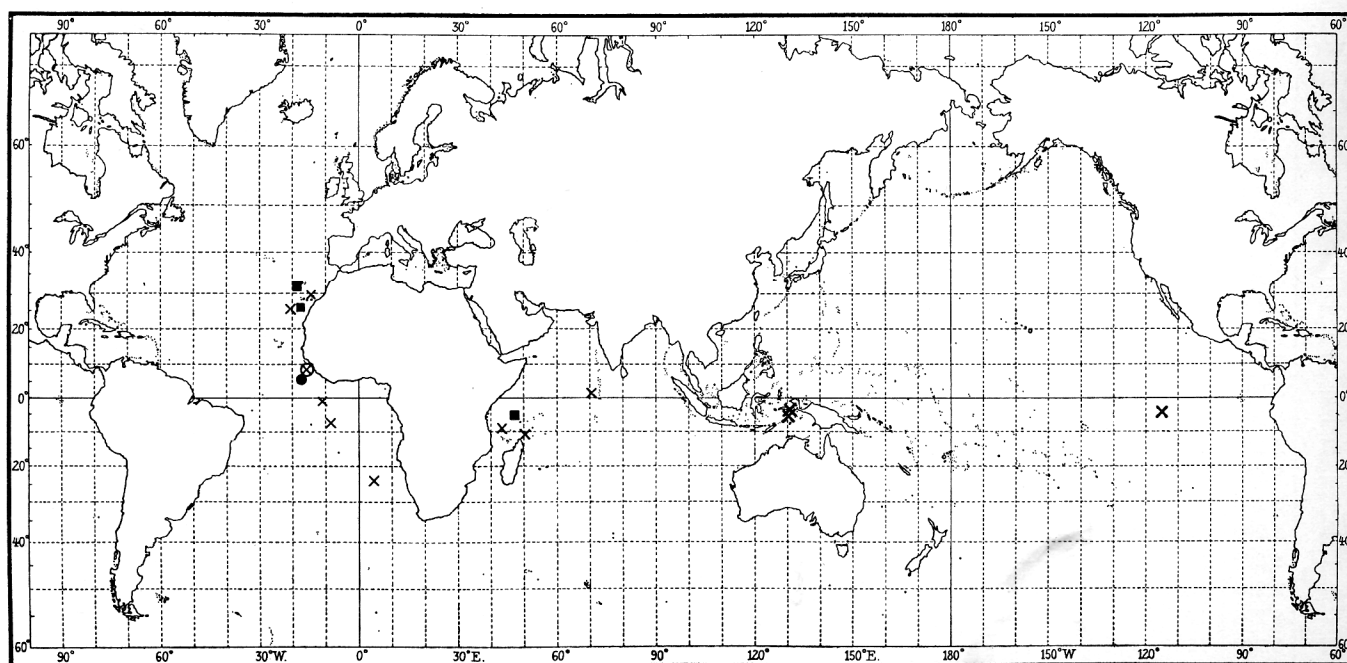
Ocean	caught	converted	measured	converted
Atlantic	1573	5635	1512	3883
Indian	2441	9522	2045	8976
Pacific	1094	4515	929	4050
Total	5108	19672	4486	16909

Amphion is about twice as numerous in the Atlantic as in the two other oceans, slightly less than double compared with the Indian Ocean and nearly three times compared with the Pacific Ocean. The insecurity of these figures must be borne in mind when drawing conclusions from them, especially because the number of actual catches in a surface haul has been multiplied with 384 for giving the converted figure.

But the figures show clearly that *Amphion* is most numerous in the Atlantic Ocean from which area the eastern part along the African coast is best investigated both by "Dana" and "Discovery". Very little is known from the middle of the South-Atlantic as well as from more coastal waters along South America. From the Atlantic Ocean the number of specimens per haul declines through the Indian Ocean and into the Pacific Ocean.

With our present knowledge it is difficult to draw any conclusions from these facts.

In Map II are shown the localities for catches of the postlarva and the adult of *Amphion*, not only from "Dana", but also for all specimens which have been recorded previously in the literature under the name of *Amphionides valdiviae* ZIMMER. Although the finds are relatively few they show a distribution similar to that of the larval form. Most of the catches of the adult and all localities for the postlarva are from the Atlantic. This is explained by the two facts: firstly, as has been shown above, that *Amphion* is twice as numerous in the Atlantic as in the two other oceans; secondly, the Atlantic is the most and best investigated of the three oceans. Therefore, there are good reasons for assuming that the postlarva will in future also be found more abundant in the two other oceans if looked for at the right depths of 2000-5000 m.



Map II. Localities with postlarvae and adult. *Amphion reynaudi*.

⊗ "Dana" postlarva I and II and adult. × "Dana" adult. ● "Discovery". ■ "Valdivia".

The individual numbers of the different larval stages do not provide much information. The numbers of larvae in the early stages are rather low because many of them due to their delicate structure have been damaged or totally destroyed in the net or during preservation and therefore to some extent can have been overlooked in the first gross-sorting of the whole material from the haul. Further, larvae seem to have been less frequently assigned to the uneven stage numbers than to the even numbers, thus in comparison with Stage IX, an extraordinarily large number of larvae have been assigned to stage X. But taken in general the numbers of specimens increase to Stage X and then naturally decrease from then on. The increase caused by spoiled material of young stages, the decrease by the general diminishing of the stock through natural mortality including predation by other organisms.

LISTS OF STATIONS WITH THEIR LARVAL STAGES OF AMPHION

For the pelagic fishery wire length paid out is given in the tables as mw. Further are noted serial numbers of stations and hauls, month, hour for the gear being set, and duration of the haul. For detailed information see the above-cited papers, (p. 5) and the list of abbreviations for types of gear used (p. 6).

In Tables XII-XIV the figures for the actual catches are given and after them with fat types the same figures converted to nearest whole figure (if below 1 raised to one) for S. 200 and duration 120 min.

Some specimens were so damaged that neither their length measurements nor their larval stage could be determined. This causes in some cases the sum of the figures under the larval stages in the tables to be smaller than the figure for the caught number in the haul.

Table XII. Atlantic Ocean. List of material. For positions and other catch data cf. The Danish Dana Expeditions 1920-22 no. 1 and Dana Reports nos. 1 and 26.

St. no.	Month	Gear	Dur. min.	Wire l. m	Numbers		Larval stages													Total									
					caught	conv.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII										
1165- 3	XI	S 150	120	600	1	2									1	2								1					
1192 -7	XII	S 200	120	100	8	8						2	2		1	1	1	1	3	3	1	1			8				
— 8	—	S 200	120	50	2	2				1	1				1	1									2				
1361- 4	VI	S 200	120	100	122	122			4	4	6	6	16	16	26	26	26	26	16	16	9	9			103				
3535- 0	VII	S 50	5	sf.	3	1152					1	384									2	768			3				
3539- 0	VIII	S 50	5	sf.	4	1536						1	384												1				
3542- 0	VIII	S 50	5	sf.	2	768			1	384															1				
3547- 3	VIII	S 200	60	100	1	2												1	2						1				
3979- 4	II	S 200	120	100	1	1																	1	1	1				
— 5	—	S 200	120	50	4	4													2	2		2	2		4				
3980-11	II	S 150	120	1000	1	2						1	2												1				
3981 -2	II	S 200	120	600	1	1													1	1					1				
— 3	—	S 200	120	300	2	2																1	1		1				
— 4	—	S 200	120	100	3	3																		2	2	2			
— 5	—	S 200	120	50	15	15						1	1		2	2		5	5	2	2	3	3	1	1	14			
3994- 1	II	S 200	60	200	6	12					1	2			2	4			2	4			1	2		6			
— 2	—	S 200	60	100	14	28			1	2	1	2	3	6		2	4		4	8						12			
— 3	—	S 200	60	50	13	26									2	4		1	2	4	8		4	8	2	4	13		
3996- 3	II	S 150	120	2000	4	8																1	2			3			
— 4	—	S 150	120	1500	4	8					1	2			2	4										4			
— 5	—	S 150	120	1000	4	8			2	4			1	2												4			
— 7	—	S 200	120	600	5	5							1	1	1	1		1	1	2	2					5			
— 8	—	S 200	120	300	7	7							1	1					1	1	1	1	1	1	1	6			
— 9	—	S 200	120	100	18	18												4	4	5	5	3	3	2	2	14			
— 10	—	S 200	120	50	24	24									1	1		4	4	5	5	7	7	4	4	21			
3997- 2	II	S 200	120	600	3	3									1	1					1	1			1	1	3		
— 3	—	S 200	120	300	1	1									1	1					1	1				1			
— 4	—	S 200	120	100	11	11									1	1		6	6	4	4					11			
— 5	—	S 200	120	50	547	547			2	2	2	2	17	17	30	30	56	56	65	65	139	139	103	103	28	28	37	37	516

Table XIII. Indian Ocean. List of material. For positions and other catch data cf. The Danish Dana Expeditions 1920-22 no. 1 and Dana Reports nos. 1 and 26.

St. no.	Month	Gear	Dur. min.	Wire l. m.	Numbers		Larval stages													Total				
					caught	conv.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII					
3800-4	VIII	S 200	120	100	10	10									1	1	2	2	2	2	3	3	10	
— 5	—	S 200	120	50	1	1															1	1	1	
3804-4	—	S 200	120	100	3	3							1	1			2	2					3	
3814-3	IX	S 200	120	100	20	20		1	1	6	6	1	1		1	1	2	2			4	4	20	
— 4	—	S 200	120	50	21	21		3	3	5	5			1	1	1	1	2	2	3	3	2	2	
3815-3	—	S 200	120	100	19	19		4	4	4	4	3	3	1	1			3	3	1	1		2	2
— 0	—	S 50	5	sf.	13	4992		3	1152	2	768			2	768			1	384	2	768	1	384	
3817-5	—	S 200	120	50	18	18			9	9	4	4		1	1			4	4				18	
— 7	—	S 200	120	150	5	5		2	2					1	1								8	
3821-2	—	S 200	120	600	2	2						1	1								1	1	2	
— 5	—	S 200	120	100	1	1															1	1	1	
3824-7	—	S 200	150	100	2	2															1	1	2	
— 8	—	S 200	150	50	7	6																	0	
3828-1	—	S 200	120	300	2	2									1	1	1	1					2	
— 4	—	S 200	120	100	7	7								1	1			2	2	1	1	1	6	
— 19	—	S 200	120	50	17	17		4	4	6	6	5	5			1	1						16	
3830-1	—	S 200	120	300	6	6						2	2	1	1	1	1						6	
3843-2	X	S 200	120	300	1	1								1	1	1	1						1	
— 4	—	S 200	120	200	14	14							1	1			1	1	2	2	4	4	14	
3844-3	—	S 200	120	250	2	2				2	2			1	1			1	1				2	
— 4	—	S 200	120	200	2	2																	2	
— 7	—	S 200	120	100	9	9							1	1							1	1	4	
— 8	—	S 200	120	50	7	7						1	1							1	1	1	7	
3847-2	—	S 150	180	3000	2	3											1	1			1	1	2	
3849-2	—	S 200	120	300	2	2											1	2	1	2			2	
— 3	—	S 200	120	200	6	6											2	2	4	4			6	
3850-1	—	S 200	120	600	2	2						1	1										1	
— 2	—	S 200	120	300	2	2		1	1														1	
— 3	—	S 200	120	200	10	10				2	2	1	1	1	1	1	1						6	
— 4	—	S 200	120	100	44	44				2	2	5	5	11	11	7	7	2	2	3	3	6	6	
3851-1	—	S 200	120	600	2	2						2	2									1	1	
— 2	—	S 200	120	300	12	12								1	1	1	1	3	3	2	2	1	1	
— 3	—	S 200	120	200	10	10								1	1	1	1			6	6	1	1	
— 4	—	S 200	120	100	20	20						4	4	1	1	1	1	1	1	1	1	1	20	
3854-1	—	S 200	120	400	17	17								1	1	1	1	2	2	3	3	8	8	
— 2	—	S 200	120	300	40	40							1	1	4	4	2	2	9	9	16	16	40	
3855-4	—	S 200	120	100	49	49							2	2	4	4	7	7	15	15	13	13	49	
3856-2	—	S 200	120	300	8	8							1	1	1	1	2	2			3	3	8	
3860-20	—	S 200	120	600	1	1									1	1							1	
— 22	—	S 200	120	100	6	6								1	1	1	1	2	2			1	1	
3893-3	—	S 200	90	300	1	2																	1	
— 9	—	S 200	90	50	3	5										1	2			1	2		3	
3902-5	XI	S 200	120	50	1	1								1	1								1	
3903-5	—	S 200	120	50	2	2			1	1						1	1						2	
3904-2	—	S 150	120	3000	2	4								1	2								2	
— 4	—	S 150	120	2000	1	2																1	2	
3905-5	—	S 200	90	100	1	2																	1	
3906-2	—	S 200	90	600	1	2																	1	
— 3	—	S 200	90	400	1	2					1	2											1	
— 4	—	S 200	90	300	1	2																	1	
— 5	—	S 200	90	100	2	3																	2	
3907-3	—	S 200	90	400	7	11		1	2			1	2	2	3	1	2	1	2				6	
— 4	—	S 200	90	300	1	2																	1	
3908-2	—	S 200	90	600	2	3																	2	
— 3	—	S 200	90	400	2	3			1	2													2	
— 4	—	S 200	90	300	8	12								1	2	1	2	2	3	3	5		7	

St. no.	Month	Gear	Dur. min.	Wire l. m	Numbers		Larval stages													Total	
					caught	conv.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII		
4795	VIII	S 200	40	220	2	6												1 3			1
4796	X	S 200	20	220	5	30		1 6		1 6								1 6			3
4797	I	S 200	50	201	2	5										1 2		1 2			2
4798	—	S 150	45	201	5	28		3 16										1 6			4
4799	III	S 150	50	201	7	34										1 5	1 5	3 15	1 5	1 5	7
4802	IV	S 200	25	183	2	10												1 5			2
4811	VIII	S 200	25	183	2	10												1 5			1
4813	IX	S 200	25	183	1	5										1 5					1
4815	I	S 150	45	201	17	96	1 6	4 21		3 16	2 11	1 6				1 6	1 6	1 6			14
4818	VIII	S 150	30	201	11	88						1 8	1 8	1 8	1 8	1 8	6 48	1 8			11
4819	VI	S 150	50	201	1	5				1 5											1
4820	III	S 150	40	201	2	12		1 6										1 6			2

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