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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PRINTED BY BIANCO LUNO A/S
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PRICE
35 Danish kr.

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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 Johs. 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 pereiopods, 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 pereiopods 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 sämmtlichen 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 *Eretmocaris*, all larval genera, as a tribe Haplopoda, family Hectarthropidae, in the Phyllobranchiata.

KORSCHELT 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 pereiopods 1–5 although none of his figures show these "lamellae". He further stated that the fifth pereiopod 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 pereiopod was present as an unbranched, six-jointed appendage. Zimmer regarded this specimen as a female. The other specimens without a fifth pereiopod 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 KORSCHELT & 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 propably 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 freeliving 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 pereiopods 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.