LARVAL DEVELOPMENT OF THE HERMIT CRAB, *PAGURUS ALATUS* FABRICIUS, REARED IN THE LABORATORY (DECAPODA, PAGURIDAE) [1])

BY

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INTRODUCTION

Despite the attention given to the larvae of European hermit crabs of the family Paguridae by MacDonald, Pike & Williamson (1957), Dechancé & Forest (1958), Pike & Williamson (1960), Dechancé (1961) and Dechancé (1962), only a few species have been described in detail. These include the larvae of *Pagurus bernhardus* (L.) (MacDonald, Pike & Williamson, 1957), the larvae of *Catapaguroides timidus* (Roux) and *Spiropagurus elegans* Miers (Dechancé & Forest, 1958; Dechancé, 1961; Dechancé, 1962). The gross features of larvae of other species of Paguridae from the vicinity of Great Britain are known through the studies of MacDonald, Pike & Williamson (1957) and those from the Bay of Naples from the work of Pike & Williamson (1960). None of these studies, however, were based upon larvae which had been reared from the egg to the first crab stage.

The life histories of *Pagurus alatus* Fabricus and *Pagurus prideauxi* Leach were reconstructed from the plankton by Pike & Williamson in 1960, and they found that the larvae resembled one another very closely although the adults can be separated with ease. They hatched the first zoeal stages of each species from eggs but were not able to rear them further. They found the second zoeal stages of the two species could not be distinguished from one another. They were of the opinion that they could separate the third and fourth zoeal stages. They did not include a description of the megalopa in their account for they found none in the plankton.

To resolve the uncertainties of larval identification associated with reconstruction from the plankton, this study is designed to describe in detail the complete development of *Pagurus alatus* Fabricus reared in the laboratory from the time of hatching to the first crab stage.

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METHODS

Ovigerous females of *Pagurus alatus* were collected by boatmen from Stazione Zoologica, Naples, at San Pietro di Fiat, Via Caracciolo and San Pietro Paola at various times from 18 December 1963 to 6 March 1964. They were usually collected at depths from 10 to 15 meters. *Pagurus prideauxi* were also collected from the same areas but viable larvae did not hatch from their eggs until late February. From personal communication with Mme. Beatrix Goldstein-Guidalevich, Muséum National d'Histoire Naturelle, Paris, I have recently been informed that she will describe the life history of *Pagurus prideauxi* from reared material. Therefore, this study will be limited to *Pagurus alatus.*

Ovigerous females of *P. alatus* were isolated in the laboratory in square plastic boxes filled with filtered seawater at a salinity of $37.7^0/_{00}$ like the Mediterranean where the adults were collected. The boxes were maintained on water tables and kept cool by running seawater until hatching occurred. One-hundred freshly hatched larvae were placed into ten small plastic dishes of filtered seawater at a salinity of $35^0/_{00}$ with ten larvae per dish, and kept in a temperature controlled room kept at 18°C. A continuous record was kept of the temperature in this room throughout the experiment. The larvae were fed *Artemia* nauplii hatched from California eggs.

Each dish was covered with a tight fitting plastic lid, labeled, and examined daily for exuviae, and number and stage of dead and living larvae. Living larvae were transferred daily to clean dishes of seawater and at this time given freshly hatched *Artemia* nauplii. All exuviae from the small dishes were preserved in ethanol and labeled. Mass cultures of larvae for fixation were kept in large plastic dishes and *Artemia* nauplii were added for food when the zoeae were changed each day. Each larval stage was fixed in Bouin's fixing solution at 60°C, and later maintained in 70% alcohol until drawn and dissected in ethanol and glycerine. Drawings of whole mounts were made on squared paper with the aid of a Whipple disk under a magnification of 100 ×; appendages were studied under 200 ×, and checked for details at 400 ×.

Duration of a stage was determined from time of hatching to first molt and in later stages from one molt to the next.

When a fourth zoea molted to a glaucothoe, it was isolated in a plastic dish of $35^0/_{00}$ seawater to which three small empty snail shells, previously boiled,

were added. As soon as a glaucothoe entered a snail shell those unoccupied were removed. No *Artemia* nauplii were given to glaucothoes.

Measurements of fixed larvae were made with the aid of Whipple disk which had previously been calibrated with a stage micrometer. Total length (TL) was measured from the tip of the rostrum to the terminal border of the telson, exclusive of the telson processes. Measurements from the tip of the rostrum to the posterior lateral spines of the carapace (CL) could not be measured accurately and were omitted.

RESULTS

First Zoea (figs. 1, I; 2, I)

Size. — TL mean 3.3 mm (10 specimens); duration: mean 7.6 days (59 specimens).

Description. — The eyes are sessile. The narrow and tapering rostrum extends beyond the tip of the antennal spine (fig. 1, I). Posteriorly the carapace bears

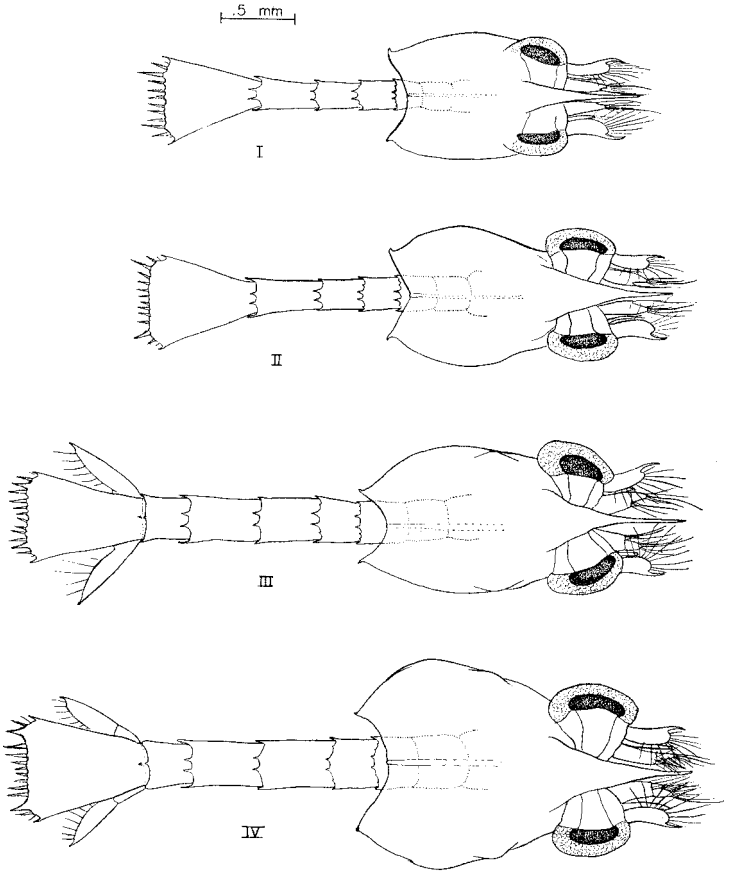

Fig. 1. *Pagurus alatus* Fabricius. Dorsal views of zoeal stages I-IV.

a short marginal spine on either side which reaches to the third abdominal somite (fig. 2, I).

The posterior margin of the first abdominal segment is smooth, but there are paired dorsal and lateral spines on the posterior ends of abdominal somites 2 to 5, with the lateral spines on the fifth somite being most prominent (fig. 2, I). On the second abdominal segment there is one lateral, two dorso-lateral denticles, and one dorsal spine on each side (fig. 1, I). On the third abdominal segment the spines are similar except there is only one dorso-lateral denticle on each side. Segments 4 and 5 lack dorso-lateral denticles. There is a very small anal spine (fig. 3, I).

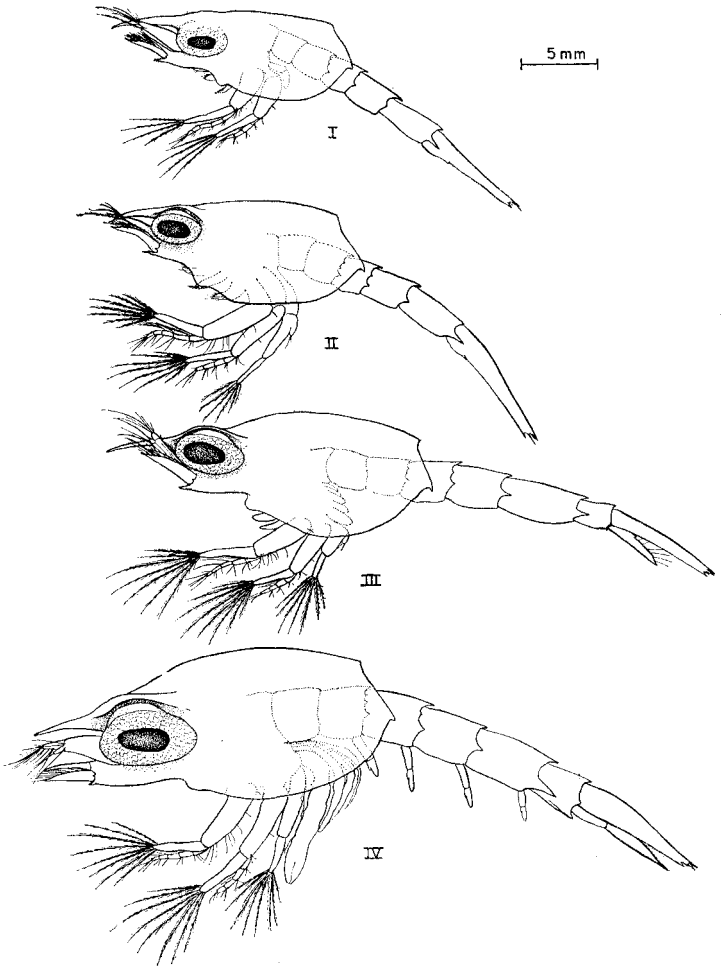

Fig. 2. *Pagurus alatus* Fabricius. Lateral views of zoeal stages I-IV.

The width of the telson is equal to the length of the telson from the anus. The posterior margin bears 7 processes on each side of a shallow central indentation; the outermost process is a tooth, the second a hair and the others articulated plumose setae (fig. 3, I). The fourth process is the largest and longest, and exceeds 1/3 the telson width. The posterior margin between the fourth processes is slightly convex (fig. 1, I and fig. 3, I).

The antennule reaches as far forward as the antennal scale minus the spine (fig. 1, I and fig. 2, I). The outer ramus bears one large aesthetasc, two medium sized processes which are more pointed but probably aesthetascs and three setae of varying lengths (fig. 4, I). There is a small inner ramus which ends in a prominent plumose seta.

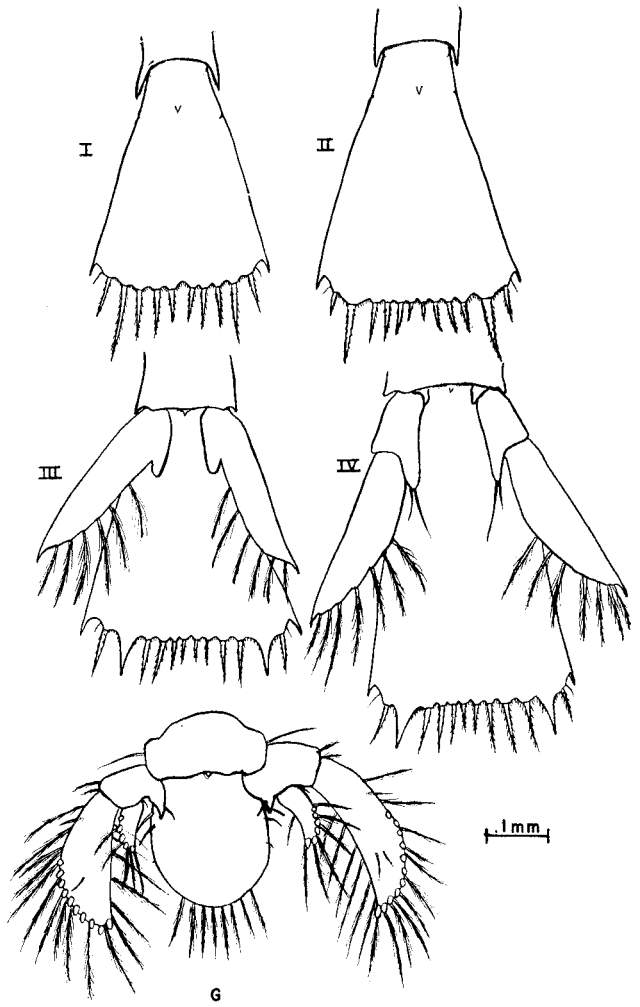

Fig. 3, *Pagurus alatus* Fabricius. Ventral views of telsons of zoeal stages I-IV and glaucothoe (G).

The outer margin of the antennal scale is concave and the inner margin is convex with 10 plumose setae (fig. 5, I). The length of the scale minus the spine is three times its maximum breadth and the basal spine on the ventral side is slightly shorter than the terminal spine. There is a prominent basal spine at

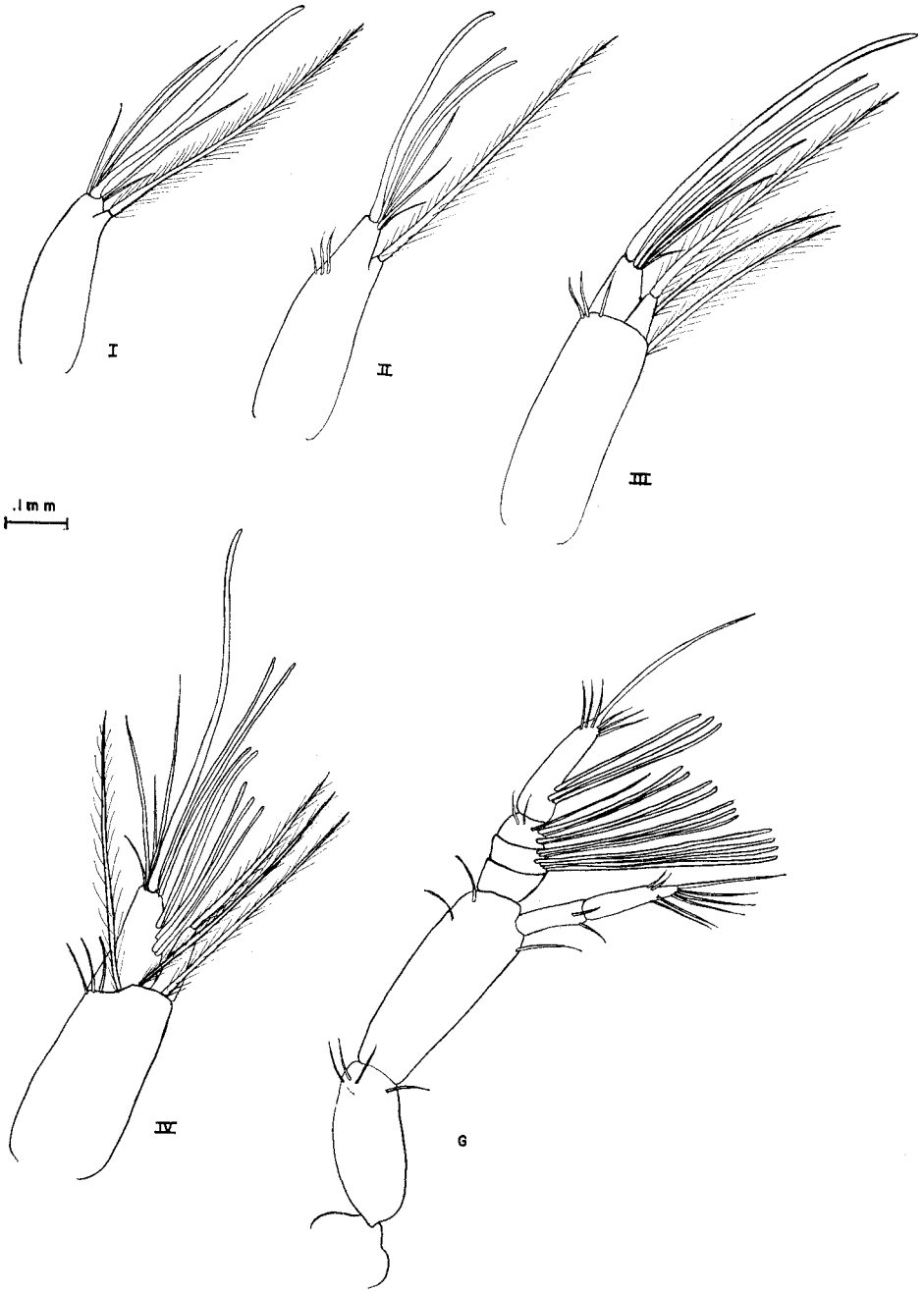

Fig. 4. *Pagurus alatus* Fabricius. Antennules of zoeal stages I-IV and glaucothoe (G).

the terminal end of the basipodite on the medial side. The unjointed endopodite bears two terminal plumose setae.

The mandibles are asymmetrical. The outer part of the incisor process of the mandible is developed into a strong tooth; other teeth are shorter and stouter (fig. 6, I). On the left side there are three separate transverse serrated ridges and a small cluster of four teeth ventral to a strong dorsal tooth.

The coxal endite of the maxillule (fig. 7, I) bears 5 plumodenticulate and two simple setae. The basal endite bears two strong spiny teeth and one minute simple seta. The endopodite is three-segmented with two short plumose setae on the distal end of the basal segment, one long plumose seta on the distal end of the middle segment, and three long plumose setae at the tip of the terminal segment.

The proximal lobe of the coxal endite of the maxilla bears 8 setae and the distal lobe bears 4 setae (fig. 8, I). The basal and distal lobes of the basal endite each bear 4 setae. Both the basal and distal lobes of the endopodite possess three setae, and there are 5 plumose setae on the scaphognathite.

The basipodite of the first maxilliped bears 9 setae as shown in figure 9, I. The unsegmented exopodite bears 4 long natatory plumose setae. The five-segmented endopodite bears three plumose setae on the medial distal surface of the proximal segment, the next three segments bear at the distal medial surface two, one and two plumose setae respectively, and the terminal segment 5 setae (fig. 9, I). Laterally the proximal three segments bear fine hair-like setules.

The second maxilliped bears one hair-like seta at the middle of the medial margin of the basipodite and a plumose seta and a stout setae with two rows of short spines on the distal-medial margin of the basipodite and the first three proximal segments of the endopodite (fig. 10, I). There are 5 plumose setae on the terminal segment. Laterally on the middle two segments of the endopodite are fine hair-like setules. There are four natatory setae on the unsegmented exopodite.

The third maxilliped consists of a rudiment of two divisions, the basipodite and homologue of the exopodite (fig. 11, I).

Second Zoea (figs. 1, II; 2, II)

Size. — TL mean 3.86 mm (3 specimens); duration: mean 5.6 days (40 specimens).

Description. — The eyes are now stalked (fig. 1, II). A medial pair of small spines has been added to the telson and thus there are 8 processes on each side of the mid-line. The posterior border between the fourth processes is straight and the median notch is not noticeable (fig. 4, II). The fourth telson process is about 1/3 the width of the telson. There are three pairs of functional maxillipeds with exopods bearing 7, 7, 6 long natatory setae respectively (fig. 2, II).

The antennule of the second zoeal stage resembles the first except three hair-like setae appear opposite the inner ramus. The two medium sized processes

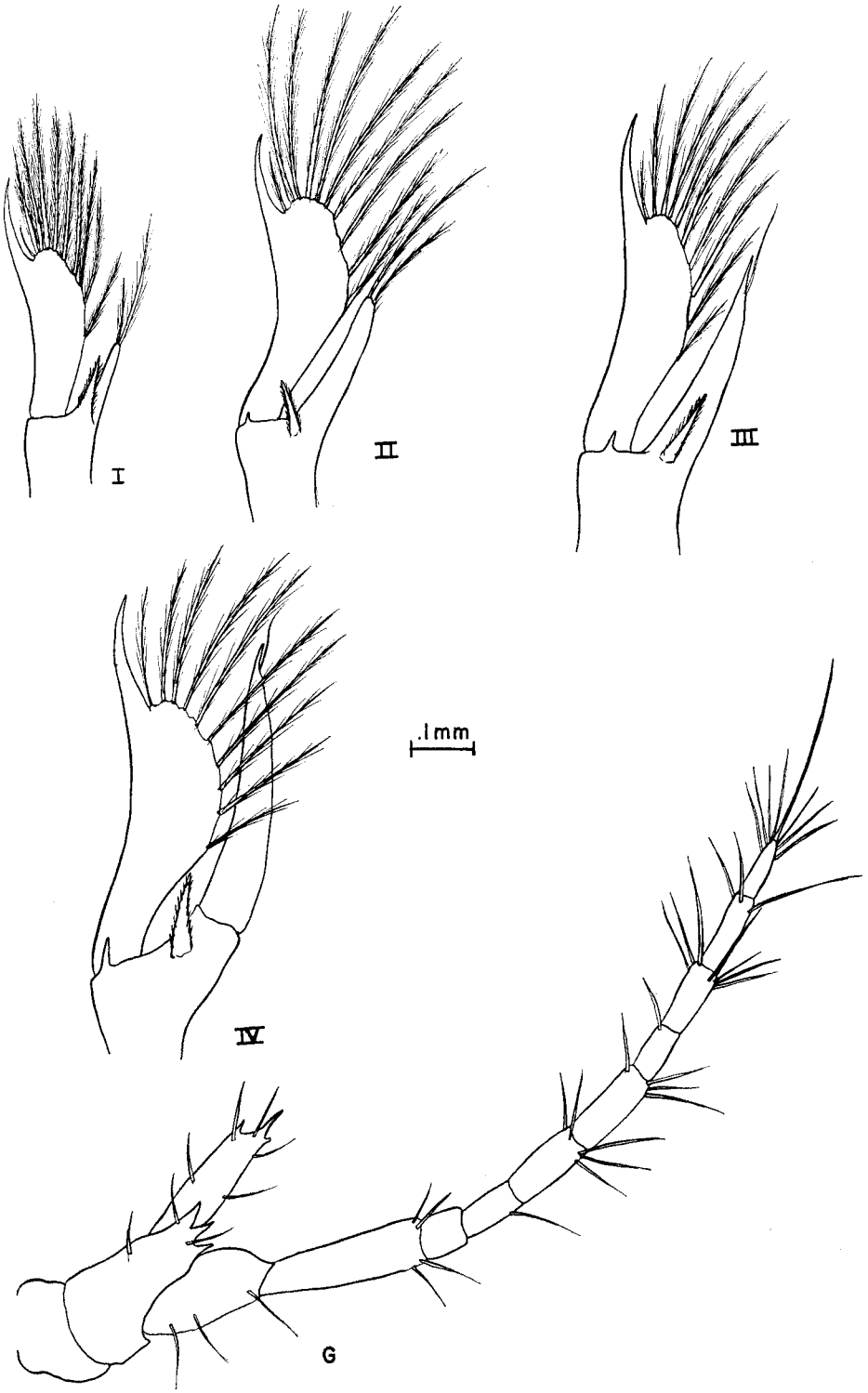

Fig. 5. *Pagurus alatus* Fabricius. Antennules of zoeal stages I-IV and glaucothoe (G).

which were pointed in the first zoea are now longer and have blunt ends and can, therefore, be recognized clearly as aesthetascs (fig. 4, II).

All parts of the antenna are larger than in the first zoea, but the endopodite is noticeably so, and the small spine at the anterior border of the basipodite is easily seen (fig. 5, II). The setation of the antenna, however, is the same as in the first zoea.

The mandible retains its same general contour, but it has more corneous teeth (fig. 6, II).

The coxal endite of the maxillule still bears 5 plumodenticulate and two simple setae, but the basal endite has four strong spiny teeth and one short simple seta (fig. 7, II). The setation of the three-segmented endopod is unchanged.

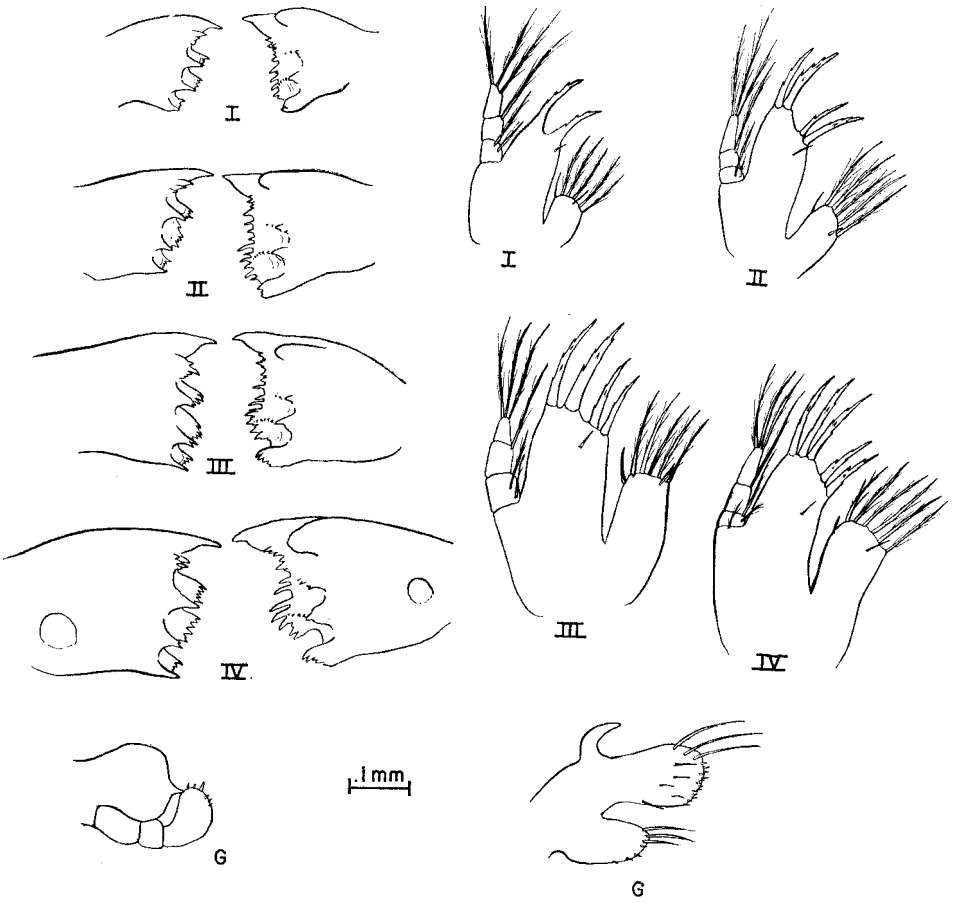

Fig. 6 (left). *Pagurus alatus* Fabricius. Mandibles of zoeal stages I-IV and glaucothoe (G).
Fig. 7 (right). Maxillules of zoeal stages I-IV and glaucothoe (G).

The proximal and distal lobes of the coxal endite of the maxilla have the same setation as in the first zoea. The basal lobe of the basal endite now has

5 setae rather than four, but the distal lobe of the basal endite and the endopodite have the same setation as in the first zoea (fig. 8, II). There are 7 plumose setae on the scaphognathite as compared to 5 in the first zoea.

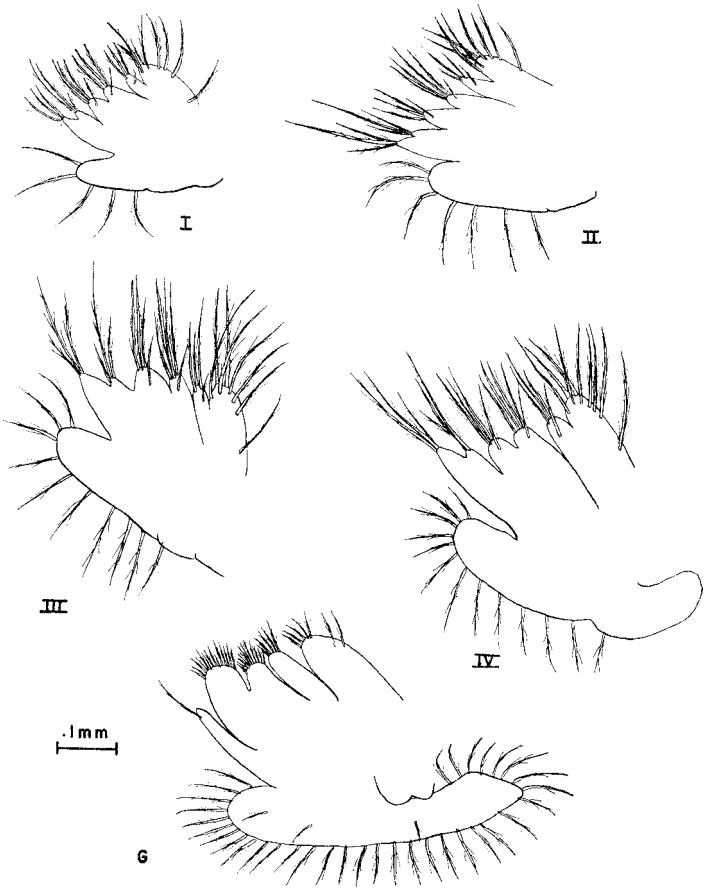

Fig. 8. *Pagurus alatus* Fabricius. Maxillae of zoeal stages I-IV and glaucothoe (G).

There are 7 natatory plumose setae on the exopodite of the first maxilliped (fig. 9, II). The setation of the segmented endopod is the same medially as in the first zoeal stage, but each of the proximal three segments now bears on the lateral surface one long plumose seta rather than fine hair-like setules. The basipodite of the second maxilliped has the same number of setae as in the previous stage. The setation of the endopodite of the second maxilliped is the same as in the first zoea except a long plumose seta appears on the middle of the penultimate segment of the lateral surface of the endopodite and a similar seta on the distal border of the antepenultimate segment. Furthermore, the exopodite now bears 7 natatory setae.

The exopodite of the third maxilliped bears 6 natatory setae and a short unsegmented endopod with two terminal setae has developed from the basipodite (fig. 11, II).

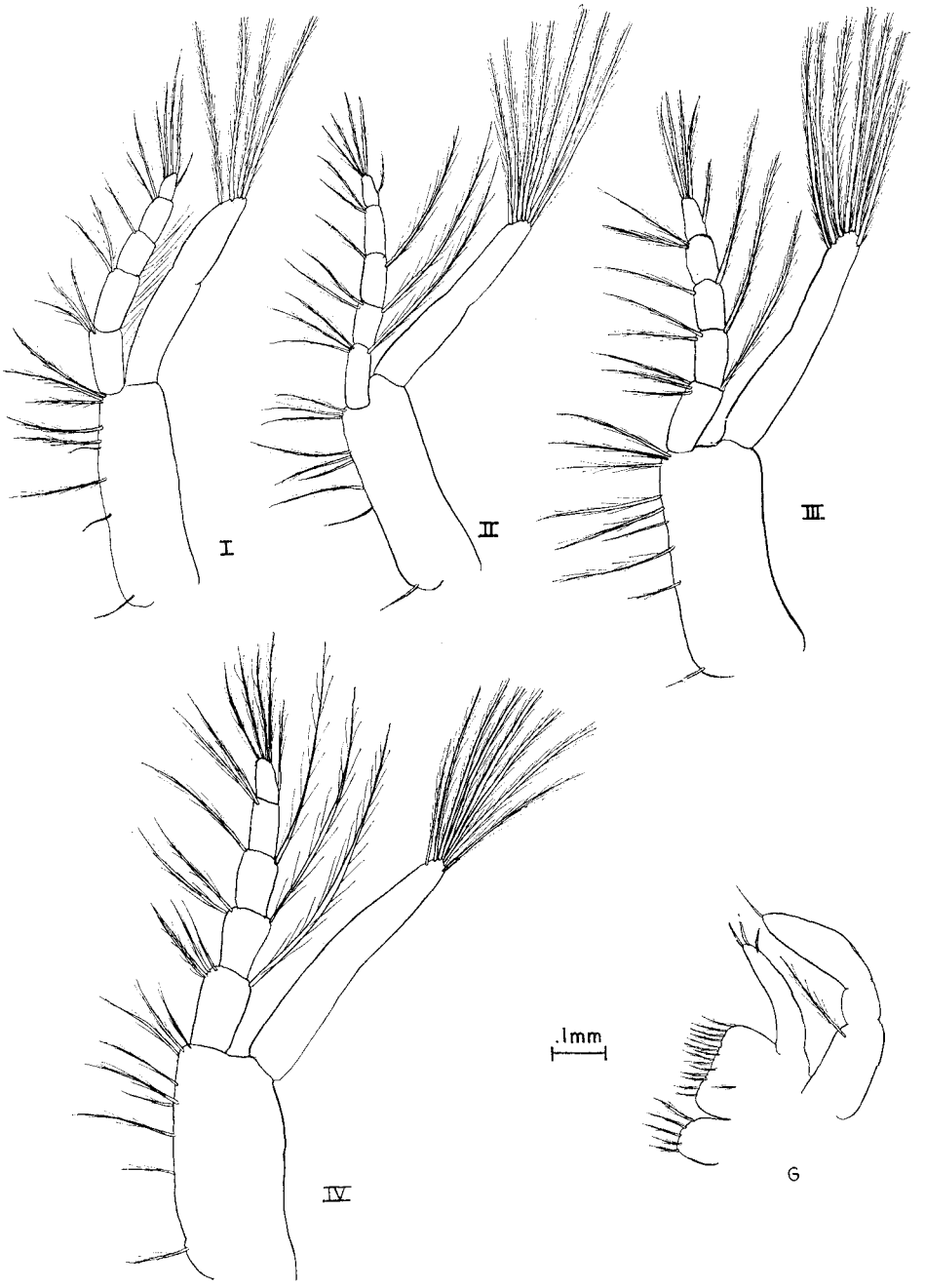

Fig. 9. *Pagurus alatus* Fabricius. First maxillipeds of zoeal stages I-IV and glaucothoe (G).

Third Zoea (figs. 1, III; 2, III)

Size. — TL mean 4.39 mm (10 specimens); duration: mean 6.5 days (31 specimens).

Description. — This stage is marked by the appearance of leg buds, a sixth abdominal segment and uropods (fig. 1, III and fig. 2, III). A small mediodorsal spine is present on the posterior margin of the sixth abdominal segment. The uropods are unsegmented, the rudimentary endopod is without setae and the exopodite, terminating in a sharp spine, bears 6 long plumose setae on its medial surface (fig. 3, III). The telson, exclusive of processes, is about as long as it is wide. There are 8 + 8 telson processes. The fourth telson process is fused with the telson and stouter than any of the other telson processes. For the first time in development it appears slightly shorter than adjacent spines (fig. 3, III) and is without barbules.

The antennule is now segmented, but the number of aesthetascs and setae on the appendage is the same as in the previous stage except two long plumose setae are added to the distal end of the peduncle just below the inner ramus (fig. 4, III).

The setation and spines of the antenna are the same as in previous stages except a long simple seta replaces two terminal setae at a subterminal position on the endopodite. The endopodite is elongated and ends in a sharp point which terminates at about the level of the distal end of the blade of the scale (fig. 5, III).

The mandibles (fig. 6, III) are larger and possess a few more teeth.

The maxillule (fig. 7, III) has the same setation as that of the second zoeal stage.

The only change noted in the maxilla (fig. 8, III) is the addition of plumose setae on the scaphognathite, bringing the number to ten.

The setation of the first, second and third maxillipeds (figs. 9-11, III) resembles that in the second zoea. The natatory setae of the exopodites of the first to the third maxillipeds number 7, 8 and 7.

Fourth Zoea (figs. 1, IV; 2, IV)

Size. — TL mean 5.27 mm (10 specimens); duration: mean 9.3 days (14 specimens).

Description. — The leg buds are larger and are partly segmented (fig. 2, IV). Bilobed pleopod buds are now present on abdominal segments 2-5 (fig. 2, IV). The armature of the abdominal segments remains unchanged (fig. 1, IV). The exopodites of the uropods articulate with the propod, but the endopodites do not (fig. 3, IV). The latter have two terminal setae. There are 7 long plumose setae on each exopodite. The length of the telson is much greater than the maximum width. There are 8 + 8 telson processes. The posterior end of the

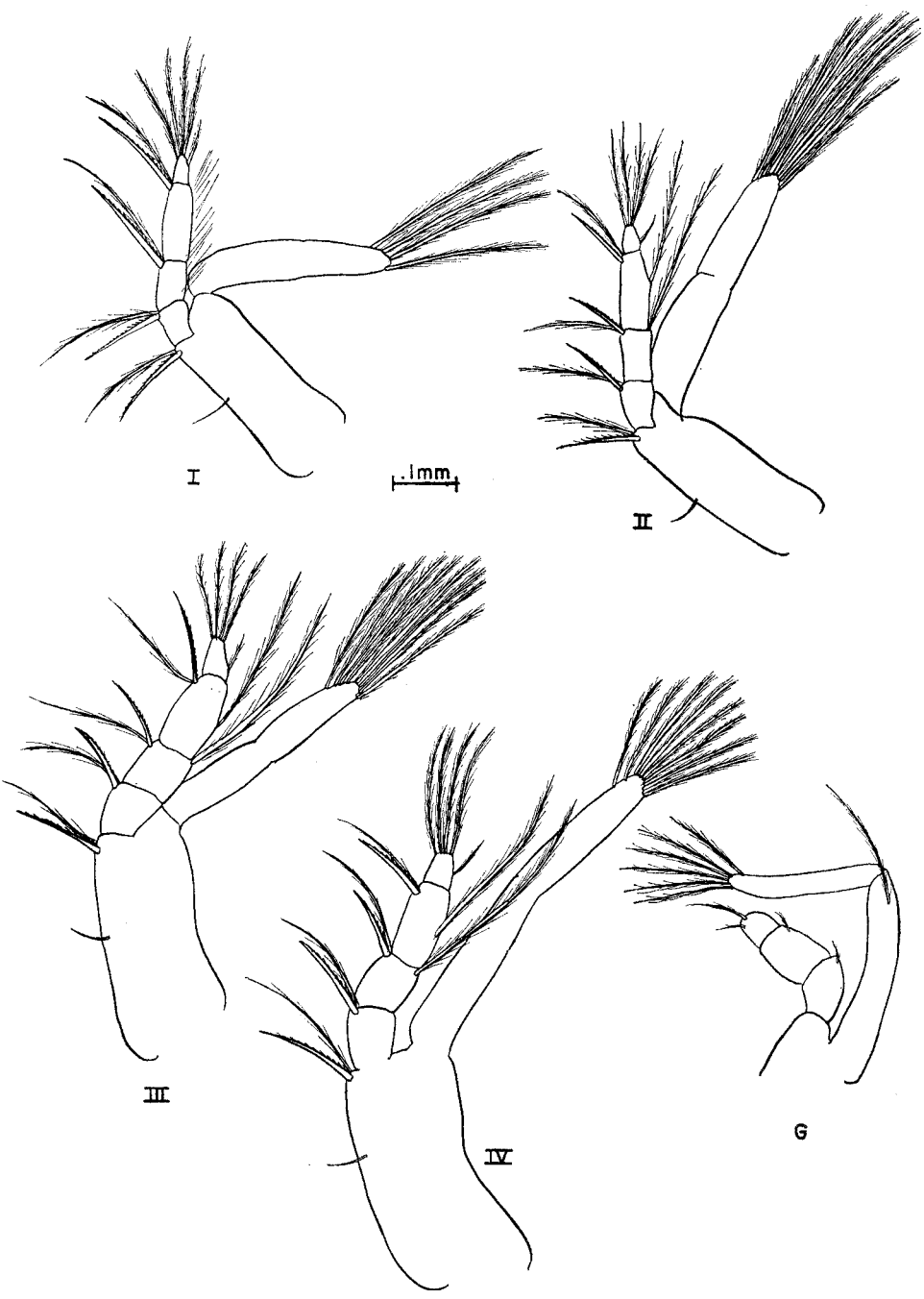

Fig. 10. *Pagurus alatus* Fabricius. Second maxillipeds of zoeal stages I-IV and glaucothoe (G).

telson between the fourth unbarbuled tooth-like processes is approximately straight (fig. 3, IV and fig. 1, IV).

At the distal end of the peduncle of the antennule there are three short simple setae and three long plumose setae. Subterminally on the medial surface of the outer ramus there are 5 aesthetascs and terminally there is one large stout aesthetasc, two medium sized aesthetascs, and four setae of different lengths (fig. 4, IV). The inner ramus is longer, but still possesses the long plumose setae it had in the third zoeal stage.

The setation and spine structure of the antennae are the same as in the third zoea but the endopod reaches to the middle of the spine of the scale (fig. 5, IV). The endopodite is now distinct from the basipodite.

The mandibles differ from other stages in that a small round mandibular bud is present (fig. 6, IV). The general arrangement of the teeth is similar, however, to those on the mandibles of the third zoea.

The coxal endite of the maxillule bears 6 plumodenticulate setae and two subterminal simple setae. The basal endite has 5 strong spiny teeth and one

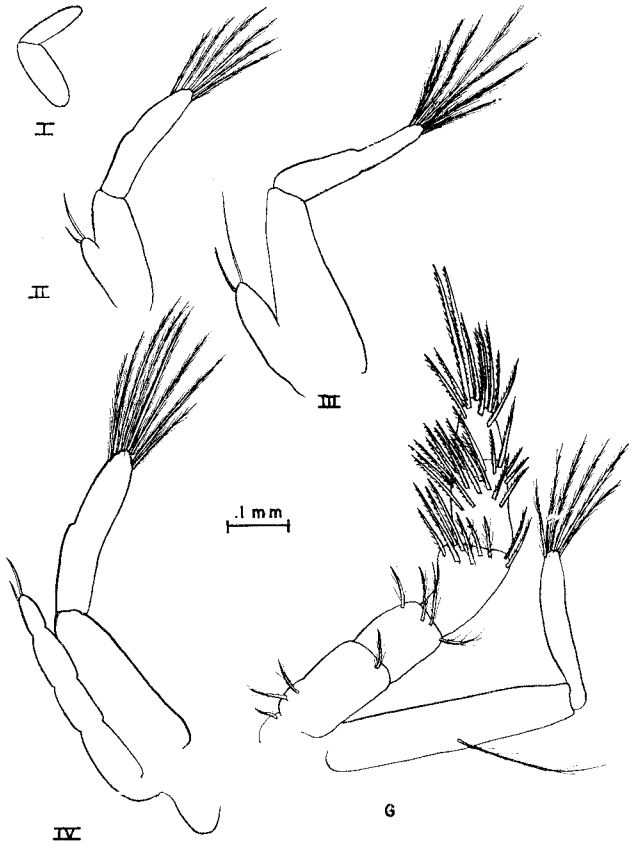

Fig. 11. *Pagurus alatus* Fabricius. Third maxillipeds of zoeal stages I-IV and glaucothoe (G).

subterminal simple seta (fig. 7, IV). The setation of the endopodite is unchanged. A short plumose seta appears on the basipodite at the base of the endopodite.

The basal coxal endite of the maxilla bears 9 plumose setae and the distal coxal endite bears four (fig. 8, IV). The proximal lobe of the basal endite possesses 5 plumose setae and the distal lobe has four. The basal and distal lobes of the endopodite each have 3 plumose setae. The scaphognathite possesses 13 plumose setae on the outer margin (fig. 8, IV).

The setation of the first maxilliped (fig. 9, IV) and second maxilliped (fig. 10, IV) are unchanged with the exception that the first maxilliped now has 8 natatory setae.

The endopodite of the third maxilliped is now partially segmented and extends beyond the base of the exopodite (fig. 11, IV). The exopodite bears 8 natatory setae.

The first pereiopod on the right side is larger than the left (fig. 13, ^{IV}1R and 1L).

Glaucothoe (fig. 12)

Size. — TL 3.4 mm; carapace length 1.4 mm; carapace width 1.44 mm; duration: mean 11.6 days (7 specimens).

Description. — The carapace is not as long as wide and not as long as the abdomen and telson together. It bears a few setae. The rostrum forms an obtuse angle with the carapace and its narrow apex extends as far forward as the subterminal spine of the ocular scales (fig. 12). The telson (fig. 3, G) is a little longer than broad. The posterior margin is convex and normally bears 8 terminal plumose setae in addition to setae on the dorsal surface.

The left uropod is larger than the right (fig. 12). The peduncle of each uropod bears a posteriorly directed spine at its base on the medial surface (fig. 3, G). There is one seta near the base of the spine, and three other setae which can be seen from the dorsal view of the peduncle. The right endopodite of the uropod bears 5 long plumose setae and up to 5 spoon-shaped corneous granules; whereas the left endopodite has 6 long plumose setae and up to 6 spoon-shaped corneous granules (fig. 3, G). On the left exopodite there are 6 long plumose setae on the medial surface and 11 long plumose setae and up to 12 spoon-shaped corneous granules on the outer dorsal border (fig. 3, G). On the right exopodite there are 6 long plumose setae on the medial surface and 11 long plumose setae and up to 10 spoon-shaped corneous granules on the outer border (fig. 3, G).

The length of the eyestalk, exclusive of the eye, is twice the width. The cornea of the eye is not wider than the eyestalk. The subterminal ocular spine extends from the peduncle of the eye to the level of the rostrum (fig. 12).

The three-segmented antennular peduncle extends slightly beyond the front of the eye (fig. 12). The middle segment of the peduncle bears four simple setae distally and the distal segment has three simple setae distally (fig. 4, G).

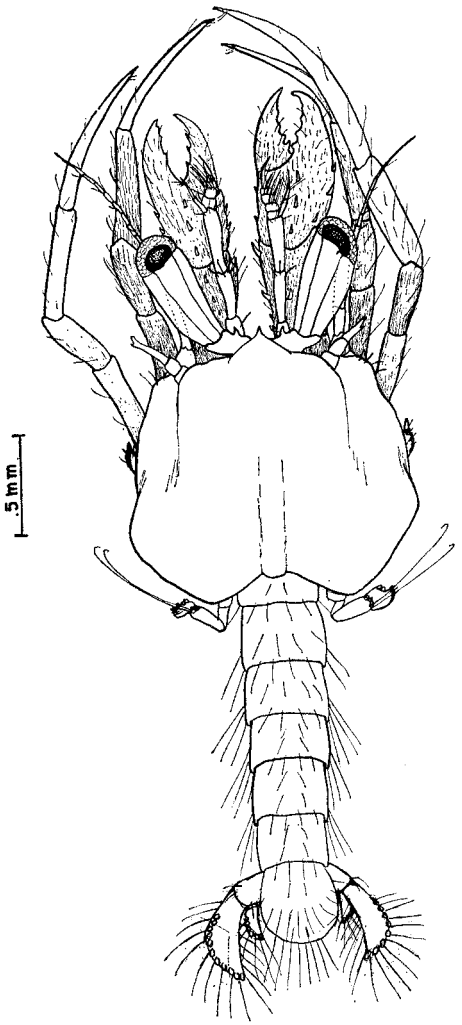

Fig. 12. *Pagurus alatus* Fabricius. Dorsal view of glaucothoe stage.

The external flagellum is composed of 4 segments with 7, 5, and 3 aesthetascs on the medial sides of the second, third and terminal segments respectively. There are also two simple setae on the third segment and 6 short setae and one long simple seta on the terminal segment (fig. 4, G). The inner flagellum is two-segmented with two short setae on the basal segment and 6 long and two short setae on the terminal segment.

The antenna (fig. 12) extends beyond the outer ramus of the antennule. The peduncle is composed of five segments and the endopodite of seven (fig. 5, G). The scale is well developed and terminates in one prominent spine and two smaller ones. The scale extends almost to the middle of the eyestalk (fig. 12).

The mandible (fig. 6, G) is a thin chitinous blade with one tooth and a three-segmented palp with 6 short spines on the distal end.

The maxillule (fig. 7, G) has lost the segmentation of the endopodite and appears as a flexed lobe. The coxal endite is rounded and possesses three terminal setae and four short spines. The basal endite has three long subterminal setae, 14 short stout spines distally and 5 setae scattered over the remainder of the lobe.

The proximal lobe of the coxal endite of the maxilla bears 5 setae terminally and two in a more basal position (fig. 8, G). The distal coxal lobe has 5 terminal setae. The proximal lobe of the basal endite bears about 11 setae and the distal lobe about 14 setae terminally. The unsegmented endopodite bears one long subterminal seta. The scaphognathite has 34 setae on the outer margin and three submarginal setae.

The first maxilliped (fig. 9, G) has a two lobed basipodite, the proximal lobe with 5 plumose setae and the distal lobe with 14 terminal setae and one subterminal seta. The unsegmented endopodite possesses three setae. The exopodite is partially segmented and bears one long plumose seta basally and one simple seta terminally.

The second maxilliped (fig. 10, G) consists of a three-segmented endopodite with a few simple setae and a two-segmented exopodite with one long plumose seta on the basal segment and 6 long plumose setae at the distal end of the terminal segment.

The third maxilliped (fig. 11, G) is the best developed of the three. The stout five-segmented endopod is characterized by numerous barbed setae on the dactylopod, propod and carpopod and plumose setae on the meropod and ischiopod. The two-jointed exopod has one long plumose seta on the basal segment and 6 long terminal plumose setae on the distal segment.

The right cheliped appears somewhat longer and stouter than the left (fig. 12). As shown in figure 13, G_R, there are setae scattered over the surface of the segments, but they are most numerous on the claws. The dactyl has two small corneous spines on its cutting edge and there are two similar spines on the opposing claw. There are well developed corneous spines on the manus, on the carpopod and at the distal end of the meropod.

The second and third pereiopods (fig. 13, G_2) resemble each other and have dactylopods which are 2/5 longer than the propod. The terminus of the dactylopod is corneous.

The fourth pereiopod (fig. 13, G_4) bears scattered simple setae on all segments. The propod has a single row of spoon-shaped corneous spines. The dactylopod is short and terminates in a stout corneous tip.

The fifth pereiopod (fig. 13, G_5) is weakly chelate, and bears ten spoon-shaped corneous spines plus two very long curved spines on the distal end of the propod, two medium sized curved spines on the medial surface plus a number of short simple setae. On the dactyl there are two spoon-shaped corneous spines plus two blunt corneous teeth and a number of setae.

Fig. 13. *Pagurus alatus* Fabricius. IV zoeal stage: IV_{1R}, cheliped of right side; IV_{1L}, cheliped of left side. Glaucothoe: G_{1R}, first leg, right side; G_{3R}, third leg of right side; G_4, fourth leg; G_5, fifth leg; G_p, pleopod.

Paired biramous pleopods (fig. 13, G_p) are present on abdominal segments 2 to 5. The endopods bear three hooked setae. The exopods of the second through the fifth pleopods bears 9, 8, 8 and 6 long plumose setae respectively.

DISCUSSION

Both *Pagurus alatus* and *Pagurus prideauxi* were reared in the laboratory from egg to the first crab stage. Each had four zoeal stages and one megalopal stage as do the life histories of all members of the family Paguridae which have been reconstructed from the plankton by investigators, such as MacDonald, Pike & Williamson (1957) for British pagurids, Pike & Williamson (1960) for Bay of Naples species, Dechancé & Forest (1958), and Dechancé (1961 and 1962) for Mediterranean pagurids. Shenoy (1967), however, found that the Indian hermit crab, *P. kulkarnii* Sankolli, had but three zoeal stages when reared in the laboratory. Shenoy believes this discrepancy is because the life cycles of British species were reconstructed from the plankton, whereas *P. kulkarnii* was reared in the laboratory. He was apparently not aware that species of *Pagurus* which had been reared, such as *P. bernhardus* (L.) (Bookhout, 1964) and *P. marshi* Benedict (Provenzano & Rice, 1964), have four zoeal stages. Since the publication of Shenoy (1967), Scelzo & Boschi (1969) found that *P. exilis* Benedict, when reared in the laboratory, also has four zoeal stages and a megalopal stage. It is not known why *P. kulkarnii* has but three zoeal stages. However, evidence deduced from other rearing studies does not support the contention that *P. kulkarnii* has but three stages because it was reared in the laboratory.

Pike & Williamson's (1960) descriptions of four zoeal stages of *Pagurus alatus* from the Bay of Naples was based on laboratory hatched material for the first zoeal stage and larvae collected in the plankton for the second through the fourth zoeal stages. They found no megalopa and described none. Their descriptions of the general morphology and chromatophore pattern of the first zoeal stage was accurate and agreed with the findings in this study. They did not attempt to describe all larval appendages of each stage, and hence, it is difficult to determine whether their reconstructions were based on *P. alatus* or not. There were the following main discrepancies in zoeae between their observations and mine: (1) they found that the rostrum reaches as far as the tip of antennal spine and in this study the rostrum extended beyond tip of antennal spine; (2) they reported that the number of natatory setae on the three maxillipeds of the third zoea was 7, 7, 7, but in this study it was 7, 8, 7; (3) they found no medio-dorsal spine on the sixth segment in the third zoea, but it was present in this study; (4) they found no evidence of a mandibular palp in any zoeal stage, but in this study the bud of the mandibular palp developed in the fourth zoeal stage.

MacDonald, Pike & Williamson (1957) divided the larvae of the British species of *Pagurus* into two groups (A and B) according to 12 larval characters. *P. alatus* has at least 9 of the 12 characters of group B to which *P. prideauxi*, *P. cuanensis*

the first zoeal stage rather than 9 as reported by MacDonald, Pike & Williamson (1957) for all species belonging to group B. Provenzano & Rice (1964) reported 9 to 11 setae on the medial side of the scale of *P. marshi* reared in the laboratory. Furthermore, *P. alatus* developed the bud of a mandibular palp in the fourth zoeal stage unlike other species belonging to group B. A third group, C, of the subfamily Pagurinae includes *Anapagurus, Spiropagurus* and *Catapaguroides.* Provenzano & Rice (1964) found *Pagurus marshi* larvae resembled *Catapaguroides timidus* (Roux), studied in great detail by Dechancé (1961), more than it did to *P. bernhardus*, a member of group A. Hence, it may be too early to divide the two groups included in *Pagurus* into two different genera based on differences in larval characters as suggested by MacDonald, Pike & Williamson (1957). The author agrees with Dechancé (1961) that *Pagurus* constitutes a heterogeneous group, and that until there are more thorough studies on the development of pagurids, including precise descriptions of all the appendages of diverse species, there is not much possibility to put to test a comparison of ideas concerning phylogeny of Pagurinae based on larval characters.

The description of the complete larval development of *P. alatus* given in this paper permits a comparison with the detailed accounts of the life history of *Pagurus marshi* by Provenzano & Rice (1964), *Pagurus kulkarnii* by Shenoy (1967) and *Pagurus exilis* by Scelzo & Boschi (1969). There are many points of similarity which are larval characters of Anomura and Paguridae according to Pike & Williamson (1960). The characters, which when considered together allow one to separate species of subfamily Pagurinae, include the outer ramus of the antennules, coxal lobe of the maxillule, scaphognathite of maxilla, character of the third maxilliped, and number of natatory setae on the exopodites of the first, second and third maxillipeds.

A tabulation of the differences in these appendages of recently studied species of *Pagurus* from the Mediterranean, Caribbean, South Atlantic and Indian Ocean will reveal that these species can be separated easily if all appendages are carefully examined.

Although the inner ramus of the antennules of these species are similar, the number of setae and aesthetascs on the outer ramus are different enough to separate one species from another in every stage of development (see table I).

It is also conceivable that the coxal endite of the maxillules is different in each species (see table II). However, until each investigator uses uniform terminology for different types of setae, as Thomas, 1970, suggests, it will be difficult to determine the extent of the difference.

It is apparent from the descriptions of *P. marshi* by Provenzano & Rice (1964), that the curved setae in the first three zoeal stages (table II) become plumose in the fourth zoeal stage, or they have been plumose throughout zoeal development as shown in their figure 6. Scelzo & Boschi (1969) describe the setae on the coxal endite as spiny (table II), but their figures show most, if not all, to be plumose. Shenoy's (1967) setae also appear to be represented as plumose.

TABLE I

Number of aesthetascs and setae on outer ramus of antennule during development of four species of hermit crabs, subfamily Pagurinae

Species Location Author	*Pagurus alatus* Mediterranean Bookhout	*Pagurus marshi* Caribbean Provenzano & Rice (1964)	*Pagurus exilis* S. W. Atlantic Scelzo & Boschi (1969)	*Pagurus kulkarnii* Indian Ocean Shenoy (1967)
Zoea I	3 aesthetascs & 3 setae	2 aesthetascs & 1, 2, or 3 plumose setae	2 aesthetascs & 2 plumose setae	2 aesthetascs & 3 setae
Zoea II	3 aesthetascs & 3 setae	2 aesthetascs, 2 plumose & 1 simple setae	2 aesthetascs & 2 plumose setae	3 aesthetascs & 2 setae
Zoea III	3 aesthetascs & 3 setae; 2 long plumose setae added distal end of peduncle	2 or 3 aesthetascs, 2 plumose, 1 or 2 small setae	3 terminal aesthetascs; 2 subterminal aesthetascs, & 3 plumose setae	3 aesthetascs & 2 plumose setae
Zoea IV	Terminally 3 aesthetascs, & 4 setae; subterminally 5 aesthetascs on outer margin	Terminally 3 aesthetascs, & 2 simple setae; subterminally 4 aesthetascs in a row	3 terminal aesthetascs; 2 subterminal aesthetascs, & 3 plumose setae	No 4th stage
Glaucothoe	4 groups of 7, 5 & 3 aesthetascs on 2nd, 3rd and terminal segment respectively	Not described	Approximately 13 aesthetascs in a row along border of 2nd, 3rd, & terminal segment	11 aesthetascs and 4 terminal setae

TABLE II

Setation of coxal endite of maxillule during development in four species of hermit crabs, subfamily Pagurinae

Species	*Pagurus alatus*	*Pagurus marshi*	*Pagurus exilis*	*Pagurus kulkarnii*
Author	Bookhout	Provenzano & Rice (1964)	Scelzo & Boschi (1969)	Shenoy (1967)
Zoea I, II, III	5 plumose & 2 simple setae	4 curved & 2 straight setae (1 submarginal bristle added in 3rd zoea)	7 spiny setae	6 setae
Zoea IV	6 plumose & 2 simple setae	5 plumose & 2 non-plumose setae; 2 submarginal setae	9 spiny setae	No 4th stage
Glaucothoe	3 terminal setae & 4 short spines	Not described	Spines of coxopodite reduced	1 stout & 3 delicate setae

TABLE III

Setation of scaphognathite of second maxilla during development in four species of hermit crabs, subfamily Pagurinae

Species Author	*Pagurus alatus* Bookhout	*Pagurus marshi* Provenzano & Rice (1964)	*Pagurus exilis* Scelzo & Boschi (1969)	*Pagurus kulkarnii* Shenoy (1967)
Zoea I	5	5	5	5
Zoea II	7	7	6	6
Zoea III	10	8 or 9	10	8
Zoea IV	13	9	15	No 4th stage
Glaucothoe	34	Not described	Lobe surrounded by setae	26

TABLE IV

Major changes in development of third maxilliped in four species of hermit crabs, subfamily Pagurinae

Species Author	*Pagurus alatus* Bookhout	*Pagurus marshi* Provenzano & Rice (1964)	*Pagurus exilis* Scelzo & Boschi (1969)	*Pagurus kulkarnii* Shenoy (1967)
Zoea I	Rudiment — 2 divisions, basipodite & exopodite	Unsegmented rudiment	Two segmented rudiment	Rudimentary bud
Zoea II	Short unsegmented endopod with 2 terminal setae develops from base of basipodite	Endopod has not developed	Endopodite develops with 2 terminal plumose setae from base of basipodite	Endopod rudimentary, small, with 2 hair-like processes; develops from distal end of basipodite
Zoea III	Same as in 2nd zoea but bigger	Endopod with 2 terminal plumose setae develops from base of basipodite	Endopodite appears same as in 2nd stage	Endopod rudimentary with 2 plumose setae; extends slightly beyond articulation of exopodite
Zoea IV	Endopodite with 2 setae; is partially segmented and extends beyond articulation of exopodite	Endopod carries one plumose & one naked seta; extends just beyond articulation with exopodite	Endopodite with 3 plumose setae extends from articulation with exopodite to a little over half the length of the exopodite	No 4th stage

(cf. MacDonald, Pike & Williamson, 1957) and *P. marshi* (cf. Provenzano & Rice, 1964) belong. The prezoea was not studied, and hence, it is not known whether the prezoea has 7 pairs of telson spines or not, the first zoeae do. *P. alatus* reared in the laboratory had 10 setae on the medial side of the scale in

The number of plumose marginal setae on the scaphognathite of the second maxilla may be of importance in separating species in the later stages as shown in table III.

Table IV reveals that there are differences in the development of the third maxilliped in *P. alatus, P. marshi, P. exilis* and *P. kulkarnii.*

The characters which may be used to identify glaucothoes of subfamily Paguri-nae include the shape of the rostrum, ocular scales, length of eyestalk versus width, and character of appendages, especially the antennules, antennae, pereiopods, pleopods and uropods. The respect in which these characters differ in *P. alatus, P. exilis* and *P. kulkarnii* may give some indication of their usefulness in the identification of glaucothoe generally. Since Provenzano & Rice (1964) were unable to rear *P. marshi* through the glaucothoe stage, the comparison with *P. alatus* is limited to pereiopods and pleopods from several partially molted fourth stage zoeae into glaucothoes.

The rostrum of the glaucothoe of *P. alatus* forms an obtuse angle with the carapace and its narrow apex extends as far forward as the sub-terminal spine of the ocular scale. The rostrum of *P. exilis* extends anterior to the ocular spines and forms an acute angle with the carapace. The rostrum of *P. kulkarnii* is short and blunt.

The ocular spines of *P. alatus* are subterminal, those of *P. exilis* are terminal and none were observed in *P. kulkarnii.* In *P. alatus* the eyestalk minus the eye is about two times longer than wide, whereas in *P. exilis* the length is about equal to the width, and in *P. kulkarnii* they are slightly longer than broad.

The number and location of the aesthetascs and setae on the antennule of *P. alatus* glaucothoe differ from the number of these structures in *P. exilis* and *P. kulkarnii* as shown in table I.

The scale of the antennae of *P. alatus* is well developed and terminates in one prominent spine and two smaller ones, whereas the scales of *P. exilis* and *P. kulkarnii* are without terminal spines. The flagellum of *P. alatus* has 7 segments, the flagellum of *P. exilis* has 14, and the flagellum of *P. kulkarnii* is composed of 6 or 7 segments.

The right cheliped in all members of subfamily Pagurinae which have been reared is larger than the left. The characters of the five pereiopods of each species, however, varies in detail. The distinguishing feature of the chelipeds of *P. alatus* is the large number of corneous spines which are present on various segments of the appendage.

The setation of the pleopods of *P. alatus* differs from that reported for *P. marshi, P. exilis* and *P. kulkarnii.* The exopods of *P. alatus*, for example, number 9,9—8,8—8,8—6,6 plumose setae on pleopods 2 to 5 respectively; those

of *P. marshi* 9,9—8,9—9,9—9,8 respectively; those of *P. exilis* 9,9—9,9—8,8—8,8 respectively; and those of *P. kulkarnii* 9,9—9,9—9,9—8,8. The endopodites bear 3 small hooks in *P. alatus*, and 2 in *P. marshi* and *P. kulkarnii*.

The characters used to distinguish glaucothoes, outlined above, should also be useful in identifying *Pagurus* larvae in the plankton.

RÉSUMÉ

Le développement du pagure, *Pagurus alatus* Fabricius récolté dans la baie de Naples, a été suivi en laboratoire à une température de 18°C et une salinité de 35‰ de l'éclosion au premier stade crabe. La durée moyenne de chacun des quatre stades zoé et du stade mégalope a été respectivement de 7,6 jours, 5,6 jours, 6,5 jours, 9,3 jours et 11,6 jours. La durée totale du développement de l'éclosion au premier crabe a varié de 38 à 42 jours.

Quatre stades zoé et une stade mégalope sont décrits. Une illustration détaillée est présentée pour montrer la séquence des changements qui ont affecté, au cours du développement aux appendices de toutes les zoés et de la mégalope.

Les soies et l'armature de la rame externe des antennules, le lobe coxal de la maxillule, le scaphognathite de la maxille et les trois maxillipèdes, aussi bien que les différences dans le développement du troisième maxillipède et la forme du telson, sont les caractères qui permettent de distinguer les zoés de *Pagurus alatus* des zoés des autres espèces de la sous-famille des Pagurinae qui ont été élevées. Les caractères utiles pour séparer les glaucothoés de *Pagurus alatus* des autres espèces comprennent la forme du rostre, les écailles oculaires, la longueur des pédoncules oculaires rapportée à leur largeur et l'ensemble des traits des appendices.

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