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THE EMBRYONIC AND EARLY LARVAL DEVELOPMENT OF *GONODACTYLUS FALCATUS* (FORSSKÅL) (CRUSTACEA : STOMATOPODA) FROM INDIA

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ABSTRACT

The embryology and early larval development of *Gonodactylus falcatus* (Forsskal) were studied, based on eggs reared and hatched in the laboratory. The larval development was followed up to the fourth larval stage when all the larvae died. Observations on the behaviour of larvae, their feeding habits and moulting periodicity were also made. Differences in the larval characters between the present series and the ones described earlier have been discussed.

INTRODUCTION

THE FIRST major contribution to stomatopod embryology is from Komai (1924), who studied the embryology of *Oratosquilla oratoria* (de Haan) in some detail. He reported the external changes that take place during the embryonic development and designated 11 stages. The early larval development of *Gonodactylus falcatus* (Forsskål) was first studied by Gurney (1937) (as *G. glabrous* Brooks) from the Red Sea. He recognised six stages of which he missed second and fifth and he was able to trace till the third stage from the eggs hatched in the laboratory. Nair (1941) studied the embryology of *Harpiosquilla raphidea* and *Oratosquilla woodmasoni* from Madras Coast. He obtained some stages in both species and was able to follow the embryonic development when information from both species was put together. The work mainly dealt with the internal changes in the development of the embryo. Serene (1954) made some observations on the biology of stomatopods from Vietnam in which he reported on the external changes in the embryonic development of *Gonodactylus lenzi*. He also studied the larval development of three species, namely *G. falcatus* ; *G. chiragra* (Fabricius) and *G. lenzi* Holthuis. In his brief study of *G. falcatus*, he recognised three stages and named them A, B and C which were not followed from moult to moult and his stages are now considered to be composites of intermoults. Later from the Red Sea, in 1957 Gohar and Al-Kholy studied the development of *Gonodactylus falcatus* (as *G. glabrous*) from the eggs hatched in the laboratory. They studied upto the sixth stage but the last stage was obtained from a fifth stage larva taken from plankton. Manning (1963) described the external changes in the embryonic development of *G. oerstedii* from Florida. The early larval development of *G. oerstedii* has been reported by Manning and Provenzano (1963). Alikunhi (1967) reported on the post-larval development, moulting and growth of the common stomatopods of the Madras Coast. The extensive studies mainly pertain to the detailed description of post-larval stages, frequency of moults, growth and age at different sizes.

The present contribution deals with the embryonic and early larval development of *G. falcatus* from the eggs reared and hatched in

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the laboratory. The first four larval stages have been studied in greater detail with descriptions and illustrations for all stages and appendages. The embryology of this species has been studied for the first time in some detail. Even though larval development of this species has been studied elsewhere, this is the first attempt from the Indian Coast. As pleopodal setae are now considered useful in identification of larvae, detailed studies for the first time on them have been made. The differences observed during the present studies from that of earlier workers have been discussed.

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Material and Methods

A female specimen of *G. falcatus* along with the egg mass was collected at Mandapam, Gulf of Mannar on 27th December 1966, by breaking open a sand-stone. The animal jumped out holding its egg mass which was shed when it jumped on sand. The animal and the egg mass were immediately put in a bottle with sea water and it soon grabbed the egg mass. The animal was brought to the laboratory and kept in fresh sea water.

The egg mass was nearly rounded in shape and was about 2 cm in diameter. It was separated from the animal and the eggs which were bright yellow in colour were divided into small groups and reared in glass troughs using filtered sea water. The water in the glass troughs was changed daily

The air and water temperatures during the present studies varied from 25°C to 28°C. The salinity of sea water varied from 27.22‰ to 30.85‰.

After hatching, a few larvae were reared individually in four inch finger bowls and water was changed daily. The larval condition whether moulted, alive or dead was daily noted. By this method the larval moulting periodicity was studied. The remaining larvae were reared in glass troughs. The freshly killed embryos and larvae were dissected under a binocular microscope, and drawings were made by using a camera lucida. Ocular micrometer was used for measurements. For total length the larvae were measured from the tip of rostrum to the median posterior margin of telson and for carapace length from the tip of rostrum to the median posterior margin of the carapace. The embryos and larvae were preserved in 5% neutral formalin.

Description

Embryology

The eggs were in the advance stage of development when they were collected and they ranged from 0.78 to 0.81 mm in diameter. The egg mass approximately contained 1000 eggs.

On 27-12-1966, when the eggs were collected, the embryo had the following characters. Eyes (Fig. 1 a) clearly demarcated; major portion of embryo covered by yolk ; abdomen curved ; segmentation faintly visible ; antennule (Fig. 1 b) elongated, unsegmented and bifid ; outer lobe bears 3 minute bristles ; antenna (Fig. 1 c) in the form of a single lobe bent backwards ; first maxilliped (Fig. 1 d) small without any segmentation ; second maxilliped (Fig. 1 e) elongated ; unsegmented and bent ;

buds of other maxillipeds present ; telson (Fig. 1 f) clearly bifid.

On 29-12-1966, further developments were noticed (Fig. 1 g). Antennule (Fig. 1 h) more bent than in previous stage ; Antenna (Fig. 1 i) with 5 bristles ; first maxilliped (Fig. 1 j) more developed, elongated and made up of 7 segments of which the last one is the longest ; second maxilliped (Fig. 1 k) with 5 segments of which fourth is the longest ; telson (Fig. 1 l) bifid.

On 31-12-1966 the embryo (Fig. 1 m) showed reduced yolk content. Eye further differentiated with a distinct pigmented portion ; antennule (Fig. 1 n) unsegmented but the inner lobe possesses two bristles ; antenna (Fig. 1 o) with six bristles inside the previous moult.

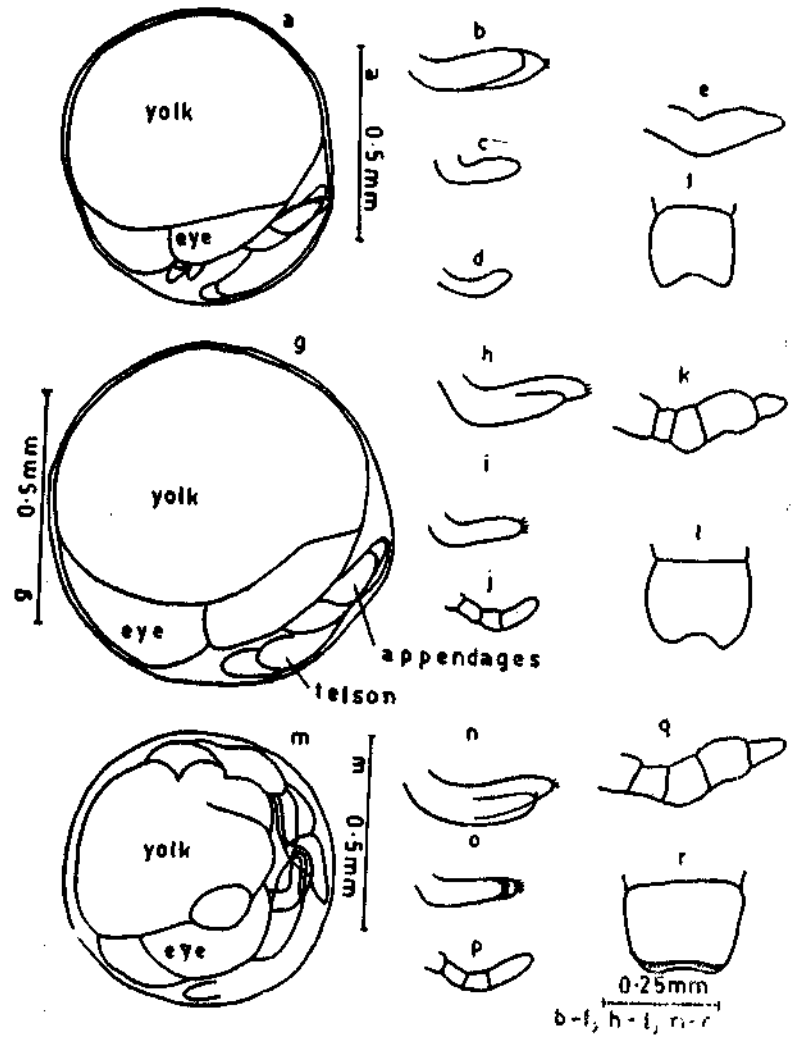

Fig. 1. *Gonodactylus falcatus* (Forsskal) : a-f. Embryo on 27-12-1966 - b. antennule ; c. antenna ; d. first maxilliped ; e. second maxilliped ; f. telson ; g-l. Embryo on 29-12-1966 - h. antennule ; i. antenna ; j. first maxilliped ; k. second maxilliped ; l. telson ; m-r. Embryo on 31-12-1966 - n. antennule ; o. antenna p. first maxilliped ; q. second maxilliped and r. telson.

In the first maxilliped (Fig. 1 p), the segments slightly more elongated ; second maxilliped (Fig. 1 q) with further developed second and third segments ; buds of pleopods very distinct ; posterior margin of telson (Fig. 1 r) slightly emarginate and nearly 10 spinules seen developing inside.

The embryo (Fig. 2 a) on 1-1-1967 exhibited the following characteristics. Rostrum appears as a projection. Posterolateral angles of carapace blunt ; antennule (Fig. 2 b) with a basal segment on which unsegmented outer and inner lobes present ; antenna (Fig. 2 c) with a constriction at base ; first maxilliped (Fig. 2 c) well developed and consists of 5 segments ; the second maxilliped (Fig. 2 e) further developed ; basal segment bears an epipodite, the appendage consists of 5 segments representing all podomeres, merus and propodus are long and dactylus short and slightly bent ; posterior margin of telson (Fig. 2 f) emarginate.

Embryo (Fig. 2 g) on 2-1-1967 is in the final stage of embryonic development. Rostrum well developed ; thoracic and abdominal region fully developed, yolk content inside the body reduced ; antennule (Fig. 2 h) with two basal segments, outer flagellum bears 6 bristles and the inner a terminal short segment with two bristles ; antenna (Fig. 2 i) possesses a basal segment and a distal segment which bears 7 bristles ; first maxilliped (Fig. 2 j) elongated and well developed ; somites of second maxilliped (Fig. 2 k) attained definite shapes, dactylus clearly bent ; telson (Fig. 2 l) with nearly 16 spinules at the posterior margin inside the moult. The diameter of eggs prior to hatching ranged from 0.83 to 0.86 mm. Embryo moults before hatching, as reported by Gurney (1937) and Gohar and Al-Kholy (1957).

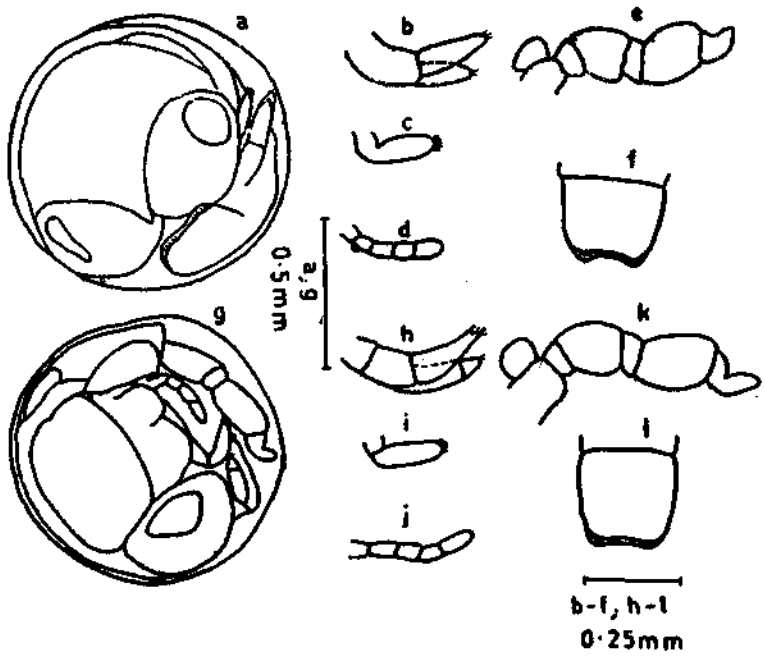

Fig. 2. *Gonodactylus falcatus* (Forsskal) : a-f. Embryo on 1-1-1967 - b. antennule ; c. antenna ; d. first maxilliped ; e. second maxilliped ; f. telson ; g-l. Embryo on 2-1-1967 - h. antennule ; i. antenna ; j. first maxilliped ; k. second maxilliped and l. telson.

Larval Development

Stage I (Fig. 3)

The larva (Fig. 3 a, b) is 2.2 to 2.3 mm long with 1.1 mm long carapace. There is a large yellow yolk mass which occupies major portion of head and thorax. Carapace longer than broad ; rostrum broad but pointed terminally and the tip extends nearly to the tip of the antennular peduncle. In lateral view (Fig. 3 b) the rostrum is seen bent over the antennule. No anterolateral spines are present ; posterolaterals large and distinct ; posterior median small. Eyes sessile and large which meet in midline.

Antennular peduncle (Fig. 3 c) three segmented ; outer flagellum unsegmented with seven setae, of which four terminal ; two stout long and two slender short and three situated on the inner aspect ; inner flagellum has a terminal small segment with two stout long and one slender short seta ; basal segment with two terminal setae. Antenna (Fig. 3 d) without flagellum ; scale broad and elongated with nine setae. Mandible and maxilla rudimentary. First maxilliped (Fig. 3 e) with five segments which are not much differentiated. Second maxilliped (Fig. 3 f) fairly large ; all segments attaining different shapes ; propodus nearly oval ; dactylus bent inwards ; epipod present at base. Third to fifth thoracic somites possess small buds representing third to fifth maxillipeds. No buds of appendages on sixth to eighth thoracic somites could be seen.

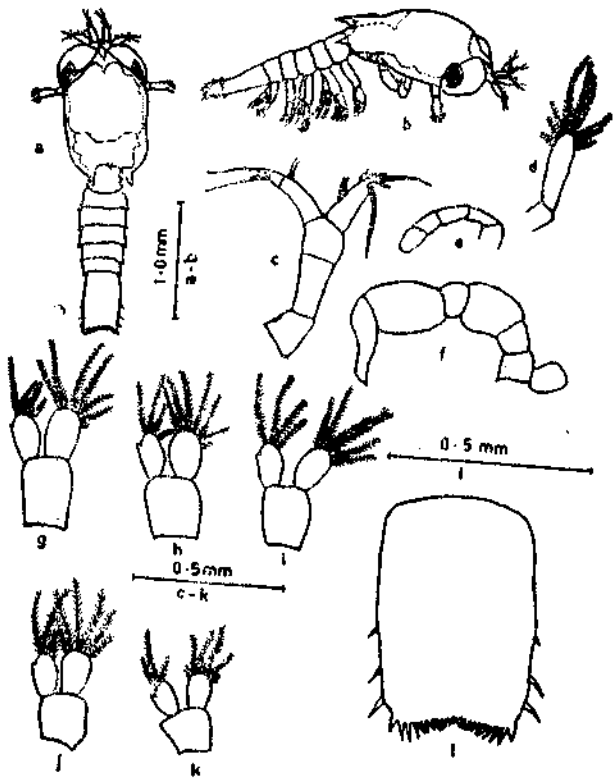

Fig. 3. *Gonodactylus falcatus* (Forsskal) : Stage I - a. dorsal view ; b. lateral view ; c. antennule ; d. antenna ; e. first maxilliped ; f. second maxilliped ; g-k. pleopods and l. telson.

First five abdominal somites nearly three times broader than long ; posterolateral corners pointed ; sixth somite not demarcated. There are five pairs of pleopods (Fig. 3 g-k) on the first five abdominal somites ; which decrease in size posteriorly. Endopods of pleopods with buds of appendix interna. The distribution of setae of pleopods is summarized in Table 1.

Stage II (Fig. 4)

Larva (Fig. 4 a, b) 2.7 to 2.8 mm long with a carapace nearly of 1.3 mm. Rostrum reaching beyond the end of antennular peduncle ; yolk mass partly consumed ; supraorbital spines make their appearance which are very minute. Posterolateral spines without basal spinules and they reach till first abdominal somite ; posterior median spine is longer than in the first stage. Eyes with short stalks.

TABLE 1. *Setation of pleopods in Stages I-IV*

Abdominal Somite		Endoped					Exopod				
		1	2	3	4	5	1	2	3	4	5
Stage I	..	4	4	4	4	3	6–6+1	6–7+1	6	6	4+1–2
Stage II	..	6	6–6+1	6	6–6+1	4+1–2	8–8+1	8–8+1	8+1	8–8+1	7+1
Stage III	..	8	8	8	8	8	9+1	10	10	10	9–10
Stage IV	..	9	9	9	9	9	10–11	11	11	11	11

n+1 or 2 indicates n setae and or two rudimentary setae

Telson (Fig. 3 l) nearly $\frac{2}{3}$ as broad as long ; with three pairs of articulated spines on the sides situated on the distal half. The length of spines increases from first to third and they are slender and sharp with the distance between them unequal. Posterolateral spines are fixed, short and stout ; with 10 + 10 or 10 + 11 spinules in between. Posterior margin of telson slightly emarginate.

Remarks : The following differences in stage I from that of earlier workers are noted. (1) Gohar and Al-Kholy (1957) reported that the outer antennular flagellum bears two inner short hairs, and the inner flagellum with an apical long, an outer, and an inner short setae ; while the present material shows that the outer flagellum bears seven setae and the inner with 5 setae. (2) They also reported 12 + 12 shorter spines in the posterior margin of telson while Gurney (1937) reported about 18 ; the present observation shows 10 + 10 or 10 + 11.

Antennule (Fig. 4 c) with three jointed peduncle ; outer flagellum with 10 setae ; four terminal, two long stout, two short slender ; six situated on inner margin ; inner flagellum two segmented ; basal segment with three setae ; of which one is long and the terminal segment with two long, stout and a slender short one. Antennal peduncle (Fig. 4 d) two segmented ; scale with 13-14 setae. Mandible (Fig. 4 e) bears three small teeth on one end of cutting edge. First maxilla (Fig. 4 f) in the form of two lobes ; coxa provided with three papillae and a spine ; basis with three papillae and a tooth. Second maxilla (Fig. 4 g) bears on its margin eight setae in four pairs. First maxilliped (Fig. 4 h) without setae ; last segment with two small papillae. Second maxilliped (Fig. 4 i) well developed ; with an epipodite at base ; dactylus reflexed on propodite.

Sixth abdominal somite faintly demarcated on the telson. Pleopod (Fig. 4 j-n) setation is summarized in Table 1.

Telson (Fig. 4 o) nearly 5/7 as broad as long ; lateral spines fixed ; small spines vary from 20-22.

Remarks : Gohar and Al-Kholy (1957) reported that the inner antennular flagellum three segmented with three short outer and one long apical setae ; but present studies show the inner flagellum two segmented ; basal segment with three setae of which one is long and the terminal segment with two long stout setae and a slender short seta.

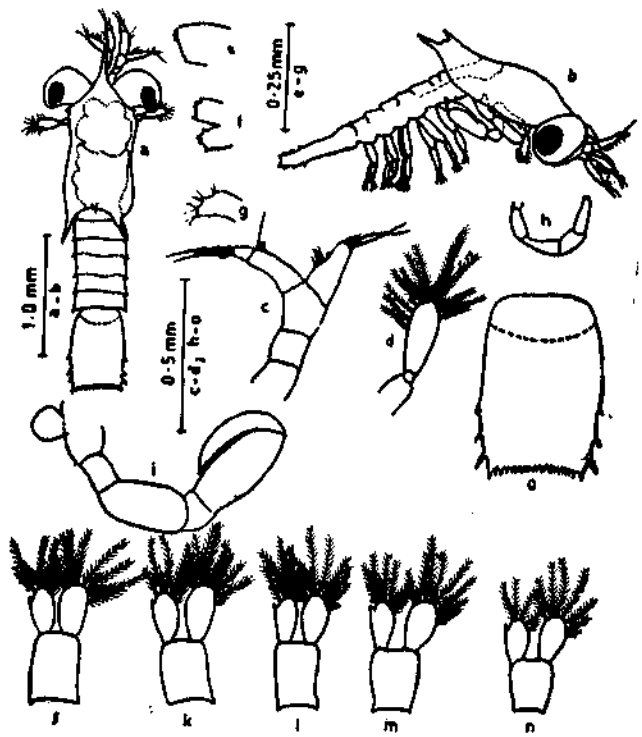

Fig 4. *Gonodactylus falcatus* (Forsskal) : Stage II - a. dorsal view ; b. lateral view ; c. antennule ; d. antenna ; e. mandible ; f. first maxilla ; g. second maxilla ; h. first maxilliped ; i. second maxilliped ; j-n. pleopeds and o. telson.

Stage III (Fig. 5)

Larva (Fig. 5 a, b) 3.2 to 3.3 mm long with carapace nearly 1.8 mm in length. Rostrum very well elongated ; tip reaches nearly to tip of antennular flagella ; a small mass of yolk still present. Supraorbital spines distinct ; posterolateral spines reach upto the middle of second abdominal somite ; distinct ventral spinules present at bases of posterolateral spines. Eyes with longer stalks than in the previous stage.

Outer antennular flagellum (Fig. 5 c) in the form of a single structure, which bears twelve setae of which two stout long ones and three slender short ones terminally placed and the rest on the inner border ; inner flagellum two segmented ; first segment bears a middle seta ; three terminal setae of which one is long and second segment with two apical long and an inner short seta. Protopodite of antenna (Fig. 5 d) with three segments, scale bears 15 or 16 setae. Mandible (Fig. 5 e) with three teeth at one end, two small ones in the middle and a blunt tooth at the other end of the edge.

Coxa and basis for first maxilla (Fig. 5 f) distinct, coxa oval in shape with five spines, basis narrower with three papillae and a large tooth. Second maxilla (Fig. 5 g) with two lateral small setae and six terminal large ones in three pairs. First maxilliped (Fig. 5 h) more elongated than in the previous stage. Second maxilliped (Fig. 5 i) well formed, propodite with few minute

Telson (Fig. 5 o) nearly 2/3 as broad as long (including the sixth abdominal somite) ; number of terminal short spines vary from 20 to 22 ; posterior margin more or less transverse.

Remarks : Gohar and Al-Kholy (1957) reported that the inner antennular flagellum is three jointed but in their figure it is shown as

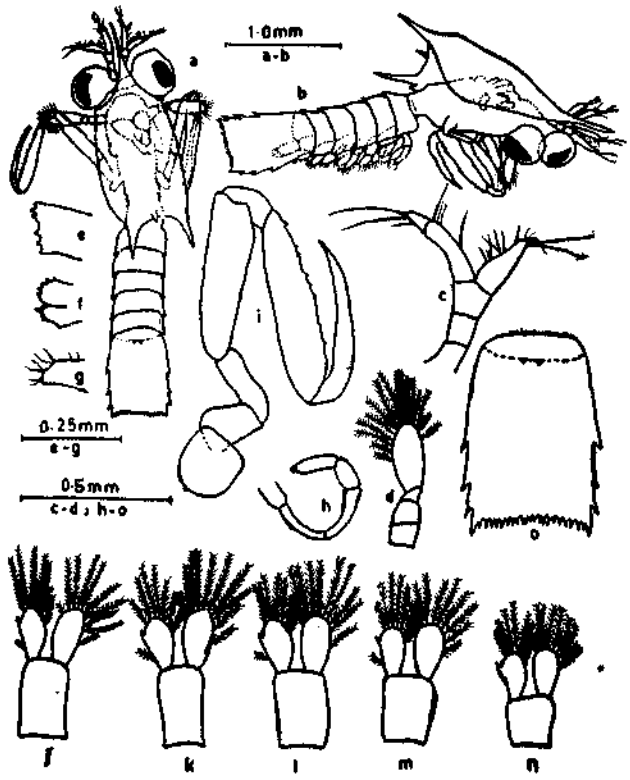

Fig. 5. *Gonodactylus falcatus* (Forsskal) : Stage III - a. dorsal view ; b. lateral view ; c. antennule ; d. antenna ; e. mandible ; f. first maxilla ; g. second maxilla ; h. first maxilliped ; i. second maxilliped ; j-n. pleopods and o. telson.

spinules irregularly situated on inner surface, and a small bud of the basal spine ; dactylus smooth.

Sixth abdominal segment partially separated from telson ; two minute median dorsal spines on hind margin present. Pleopods (Fig. 5 j-n) setation summarized in Table 1. On the endopods of the first four pleopods a seta is situated below appendix interna.

two jointed ; while the present studies indicate it to be two jointed. Further the inner flagellum is with a long apical seta an inner and four outer setae according to Gohar and Al-Kholy (1957) ; while the present studies indicate 7 setae on the flagellum. They also reported outer flagellum with six apical, outer and inner setae ; but the present observation shows twelve setae of which five terminal and seven on the inner border. Differences are also

observed in the maxillar protopodite as telson spines as compared to the description of Gohar and Al-Kholy (1957). In the present studies the former is with two lateral small setae and six terminal long ones, as against five setae described in earlier work. Telson in the present material shows 20 to 22 spines whereas it was 13 + 13 short spines in those obtained by Gohar and Al-Kholy (1957).

Outer antennular flagellum (Fig. 6 c) with distal half of the inner margin slanting ; bears nine setae of which two are terminal, one long and one short and seven on inner margin ; inner flagellum three segmented ; basal segment with one seta, middle with one long and two or three short setae ; terminal with three setae of which one stout and long ; and sometimes with a small bristle. Protopodite of antenna (Fig. 6 d) three segmented which bears a small

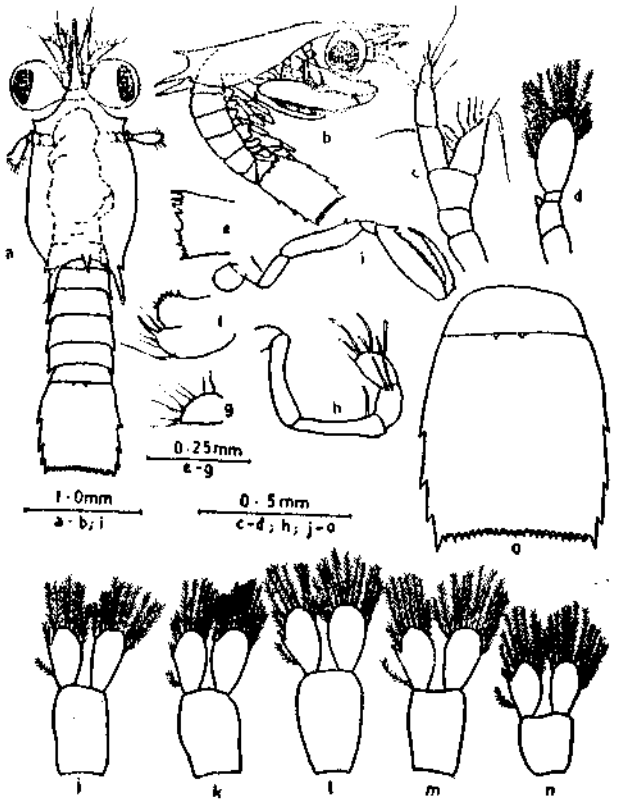

Fig. 6. *Gonodactylus falcatus* (Forsskal) : Stage IV - a. dorsal view ; b. lateral view ; c. antennule ; d. antenna ; e. mandible ; f. first maxilla ; g. second maxilla ; h. first maxilliped ; i. second maxilliped ; j-n. pleopods and o. telson.

Stage IV (Fig. 6)

Larva (Fig. 6 a, b) 3.8 to 3.9 mm long with carapace 2 mm in length. Rostrum extending beyond antennular flagella and it bears three ventral spinules. No yolk mass present ; supraorbital spines well formed ; posterolateral spines reach beyond second abdominal somite. bud representing endopod ; scale with 15 setae. Mandible (Fig. 6 e) larger than the previous stage ; incisor region with four large stout teeth ; molar region with three large teeth and three to five minute teeth. First maxilla (Fig. 6 f) with coxal part rounded with seven spines ; basis bears terminally a stout tooth

with one seta on one side, two setae on the other side and an isolated long seta. Second maxilla (Fig. 6 g) possesses eight setae of which six situated in three pairs and remaining two isolated. More developments on first maxilliped seen (Fig. 6 h) dactylus makes its appearance as a tubercle on propodus ; merus bears one seta, carpus bears two setae and propodus bears six setae in three pairs and two minute bristles near the tubercle. Second maxilliped (Fig. 6 i) well formed with epipod at base ; merus with minute seta on tubercle ; propodus with one large basal spine and about twelve spinules with a few bristles in between, on upper margin ; dactylus with proximal outer tubercle and three small bristles on cutting edge ; tip minutely serrated.

Posterolateral corners of abdominal segments produced into acute spines ; sixth segment distinct. Appendix interna of pleopods (Fig. 6 j-n) have hooks ; setation summarized in Table 1.

Telson (Fig. 6 o) 3/4 as broad as long (including the sixth abdominal somite) ; posterolateral spines well developed ; with 20-21 small spines of same size ; minute serrations present in between small spines ; posterior margin almost transverse.

Remarks : Gohar and Al-Kohly (1957) reported outer antennular flagellum with two long inner and four short apical setae ; but the present studies showed nine setae of which two, one long and one short, are terminal and seven on inner margin. The third joint of inner flagellum is with a long apical seta and second joint with a short upper and a longer outer setae according to Gohar and Al-Kohly (1957) ; while the present studies showed basal segment with one seta ; the middle with one long and two or three short setae ; and terminal with three setae of which one is stout and long and sometimes with a bristle. Differences in setation were also noticed in the maxillular palp and the propodus of first maxilliped.

Discussion

The egg mass at the time of collection was in an advanced stage of development. Manning (1963) with reference to the work of Shino (1942) has given 11 stages in the embryonic development of stomatopods. The present egg mass may be considered to be in the 9th stage as the antennules are already branched and the development of first and second maxillipeds has taken place. The present study mainly deals with the external changes but some detailed studies on appendages were also made to enable better understanding on the development of the embryo. The development in *Gonodactylus falcatus* generally agrees with the development in *G. oerstedii* as reported by Manning (1963).

During the present study it was observed that when only a few eggs were reared along with the animal and the animal was not fed, it ate its own eggs. This confirms the observations of Gohar and Al-Kholy (1957). The studies indicate that it is better to separate individual eggs or small groups of eggs rather than to rear the whole egg mass intact. When the group of eggs was large the eggs which are in the interior either did not develop or developed slowly compared to the eggs at the periphery. The use of filtered sea water minimised the ciliate attack.

On 3-1-1967 about 200 eggs had hatched. The larvae moulted into second stage on 5-1-1967, third on 7-1-1967 and fourth on 9-1-1967. The temperature of water in the glass troughs in which the eggs hatched is 26°C. The atmospheric temperature at that time was 28°C.

Larval behaviour was observed on some larvae. On the first three days the larvae remained on the bottom of the glass trough. It was observed that when torch light was focussed from the sides of the trough at night, the larvae swam away from light only during early stages. The studies indicate that the

larvae are negatively phototrophic during early stages and later become positively phototrophic.

When a large number of larvae were reared together in a single trough it was observed that sometimes 50 or more larvae formed a ball like structure by their aggregations with all heads facing the center of the ball and tails projecting away from the ball. Such smaller aggregations with 15-30 larvae were also noticed.

Gohar and Al-Kholy (1957) recommended four larval diets, (a) Plankton from which the larger animals had been removed, (b) eggs and larvae of Echinodermata and Mollusca, (c) powdered yolk of hen's eggs and (d) the powder of a cake made up of two parts by volume of flour and one part of yolk. They observed that (b) and (c) proved to be the best diets. During the present studies the following results were obtained. The larvae in the fourth stage were provided with different foods, the teased ovary of starfish, the eggs of sea urchin, the live plankton from which larger forms have been removed and the hen's egg yolk. Active feeding in none of the above instances was noticed. Manning and Provenzano (1963) also report that larvae of *G. oerstedii* were given echinoderm eggs, *Artemia* nauplii and mixed plankton without success.

There was negligible casuality in the first three stages as the larvae utilised the yolk present inside the body. In the fourth stage the larvae started dying and it may be due to the fact that they could not be induced to feed on the diet provided for them.

Gurney (1937) in his account confused with the stages in the development. Gurney's stage two is really stage three because he reported posterolateral spines with ventral spinules and telson with dorsal spines near base in stage two. These characters appear only in stage three as reported by Gohar and Al-Kholy (1957) and as observed during the present studies. Gurney's stage three is stage four of the present studies because he reported ventral spines on rostrum, antenna with rudiment of endopod, first maxilliped with dactylus which appear only in stage four.

The setation of pleopods has been found to be of considerable importance in identification of larvae in other genera and so for the first time detailed studies on this species have been made. The setal formula of *G. falcatus* varies little from the setal formula of *G. oerstedii* as given by Manning and Provenzano (1963). The number of setae on pleopods in the fourth stage of *G. falcatus* is less than that found in the same stage of *G. oerstedii*. In the second stage of *G falcatus* minute supraorbital spines are present and these are absent in the case of *G. oerstedii*. Mandibles have been reported for the first time in the second stage in *G. falcatus*. The first maxilliped in *G. oerstedii* bears three curved setae in the second stage which are absent in *G. falcatus*. Mandibles do not make their appearance even in third stage in *G. oerstedii* while it has already been formed in the stage II in *G. falcatus*. First and second maxillae in the third stage show greater differentiation in the case of *G. falcatus* and they are in the bud condition in *G. oerstedii*.

In the fourth stage of *G. falcatus* the rostrum is armed with three ventral spinules but in *G. oerstedii* four to five ventral spinules are present. Inner antennular flagellum three segmented in *G. falcatus* and two segmented in *G. oerstedii*.

Gohar and Al-Kholy (1957) have designated the first three stages as propelagic stages and the later three stages as pelagic stages. They were of the opinion that the third pelagic stage would moult to the post larva. In our present state of knowledge it is too early to presume that only six larval stages are present in the development of *G. falcatus*. The answer would only be obtained when the larvae are reared till the postlarval stage.

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