J. Mar. biol. Ass. India, 1968, **10** (1): 52-70

OBSERVATIONS ON THE DEVELOPMENT OF THE EXTERNAL GENITALIA IN SOME INDIAN PENAEID PRAWNS*

By M. J. GEORGE** and P. VEDAVYASA RAO**
Central Marine Fisheries Research Institute

IN penaeid prawns as in some other crustaceans the external sexual organs, the petasma or andricum in the male and the thelycum in the female have attained great prominence as they offer reliable characters of taxonomic differentiation of species and have attracted the attention of very early taxonomists like Bate (1888) and Kishinouye (1896, 1898 & 1900). Later Heldt (1938), Burkenroad (1939) and Kubo (1949) carried out intensive studies on the structural modifications of these organs in many species of penaeids. The latter author made extensive investigations on the morphological changes in the external genitalia of both sexes during growth and development. Eldred (1958) observed the development of the genitalia and impregnation in the pink shrimp, *Penaeus duorarum*. The development of the petasma and thelycum of the Indian prawn, *Metapenaeus dobsoni* was described by Menon (1951) during the course of his study of the early life history of the species.

With the rapid development of the prawn industry in India, extensive studies on the various aspects of the biology and habits of the economically important species are being carried out in the Central Marine Fisheries Research Institute. As a part of these studies, some observations on the structural changes in the development of the external sex organs of the commercially important species of *Penaeus indicus*, *Metapenaeus monoceros*, *M. affinis*, *M. dobsoni* and *Parapenaeopsis stylifera* have been made. Materials for the present study were obtained from the backwater and marine prawn catches off Cochin. A large number of prawns of both sexes and varying sizes were examined in each species.

GROWTH AND DEVELOPMENT OF EXTERNAL SEX ORGANS

The petasma of the male is abdominal in origin and formed by the modification of the right and left endopodites of the first pair of pleopods. Each of the petasmal endopodite is formed by two main lobes, the median and the lateral. The lateral lobe is composed of two foldings, the dorsal or anterior and the ventral or posterior lobules. In the adult prawn the two halves are generally joined together in the median line on the dorsal side by a number of minute hooks or cincinnuli arranged in a zipper-like manner. On the ventral side the two halves are usually closely approximated but not united together. The distal ends of the lobes show considerable modifications varying with species. In the development of the organ specific differences are noticed.

---

* Paper presented at the Australian/New Zealand meeting on Decapod Crustacea, Sydney, October 24-28, 1967.

** Present address : Central Marine Fisheries Research Substation, Ernakulam, Cochin-16.

In the female the external sex organ is thelycum which is thoracic in origin and formed by the modifications of sternal plates of somites XII, XIII and XIV. It is essentially composed of a median or anterior plate and a pair of lateral or posterior plates. These plates are modified in different ways in different species and serve for the attachment of spermatophores provided by males during copulation.

Penaeus indicus

Petasma : The size of postlarva at which the petasmal endopodites appear on the first pleopods is 14-15 mm. Specimen measuring 16 mm. in total length has the petasmal endopodite as a small bud-like projection, 0.035 mm in length (Fig. 1, a). At 20 mm. length the petasmal bud grows twice in length. At a size of 28 mm. length, the endopodite is finger-like and measures 0.225 mm. (Fig. 1, c). No apical hair is present in any of these stages. At 38 mm. size, the finger-shaped endopodite elongates further. In specimens measuring 48 mm. in length (Fig. 1, d) the petasma measures 0.725 mm. It is foliaceous and sub-rectangular in outline with narrow proximal stalk-like portion, the distal tip being broad and rounded. 2 to 3 small hairs are present on the inner distal border at about $\frac{1}{3}$ distance from the tip. In *P. monodon* Kubo (1949) observed these bristles at the tip. A broad notch is present on the inner proximal margin and from this point the petasma tapers proximally. A faint groove demarcating the median and lateral lobes is visible.

In the next size (55 mm.) the petasma resembles that of the preceding stage in general form, but the tip develops a shallow indentation, forming two small apical elevations representing the median and lateral lobes (Fig. 1, e). The longitudinal groove is also evident running from the emarginated tip to the notched proximal inner margin. The bristles near the tip have disappeared. In a specimen measuring 65 mm. length (Fig. 1, f) the petasmal endopodite measures 1.125 mm. The lateral lobe develops further and is slightly longer than the median lobe which has a rounded tip.

As the prawn grows to 82 mm. size, the petasma measures 1.5 mm. (Fig. 1, g). The apical depression deepens and an additional ridge appears in the median lobe, dividing this lobe into the dorsal and ventral lobules. The distal margin of the lateral lobe now gets divided into two small folds with the appearance of another indentation in that lobe, marking the beginning of the formation of the dorsal and ventral lobules of this lobe. The tip of the ventral lobule gets slightly folded inwards. In 92 mm size (Fig. 1, h) the petasma appears distally narrow. 5 to 6 small hooks develop at the inner subapical median border. The distal tips of the median lobes now enlarge and recurve medially overhanging the outer lobes. The lobules of the lateral lobes are now well developed and their tips curve inwards laterally.

As the prawn attains 105 mm. size the petasma assumes almost the adult form and character (Fig. 1, i). Hooks are now developed all along the inner margin so that the two halves are united dorsally. The curvature of the distal ends of the median lobes is more pronounced and the ridges separating the dorsal and ventral lobules are also well defined. At the sub-terminal region of this ridge some tubercles are present. Fifty per cent of the prawns had their petasmal endopodites fused at the size of 102 mm (Fig. 9). Hall (1962) observed for the same species in the Singapore prawn pond fishery, this size at 2.34 cm. carapace length (98.3 mm. in total length calculated by using his own conversion factor). The higher size

noticed in the present observations may be either due to seasonal variations as noticed by Hall (*op. cit.*) in *Metapenaeus mastersii* or geographic variation.

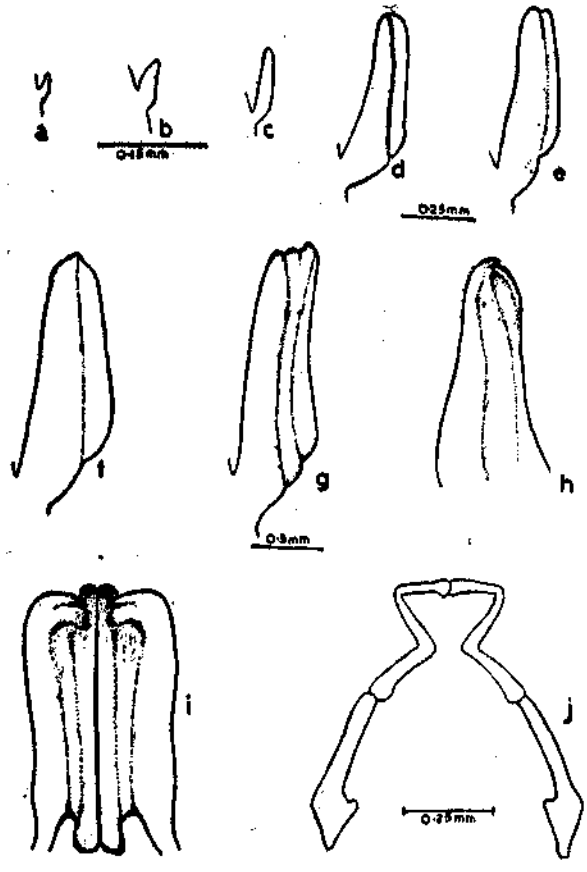

FIG. 1—Development of petasmal endopodites of *Penaeus indicus*. *a*. 16 mm body length, *b*. 20 mm, *c*. 28 mm, *d*. 48 mm, *e*. 55 mm, *f*. 65 mm, *g*. 82 mm, *h*. 92 mm, *i*. 105 mm, *j*. Cross section of adult petasma.

The development of petasma after this stage is only in the increase in size along with the growth of the animal. In cross section of the adult petasma (Fig. 1, j) both lobules of the median lobe as well as the dorsal lobule of the lateral lobe are thin and comparatively broad. The ventral lobule of the lateral lobe is broader than the dorsal lobule and situated almost at right angles. In general feature, the adult petasma has the form of a subcylindrical tube. The median lobe is membraneous and prolonged posteriorly into a rounded projection. Anteriorly this lobe has a rounded tip which curves ventrally overhanging the terminal portions of the lateral lobules, and it is sparingly tuberculated dorsally. The lateral lobe is broader and thicker than the median one. The ventral margin of the ventral lobule of this lobe is thickened and calcified. Both the ventral and dorsal lobules are distally curved inwards. The tip of the ventral lobule is narrow and acutely pointed. The terminal portion of the dorsal lobule is broader, fleshy and provided with 14 prominent teeth. The subterminal curved region of this lobule is tuberculated.

Thelycum : The development of the thelycum in this species is more or less in the same pattern as described for other species of *Penaeus* by Kubo (*op. cit.*). In prawns measuring below 30 mm body length the thelycum is hardly developed. At 35 mm size (Fig. 2, a) the median plate is discernible as a small elevation in the middle of the 7th thoracic sternite. The rudiments of the lateral plates are seen as a pair of narrow triangular plates on 8th thoracic sternite. At a length of 40 mm. (Fig. 2, b) these lateral plates are further enlarged and the median plate remains in the same condition. Differentiation of the plates becomes more clear at 45 mm size (Fig. 2, c) when the anterior plate appears as a raised portion having a rounded

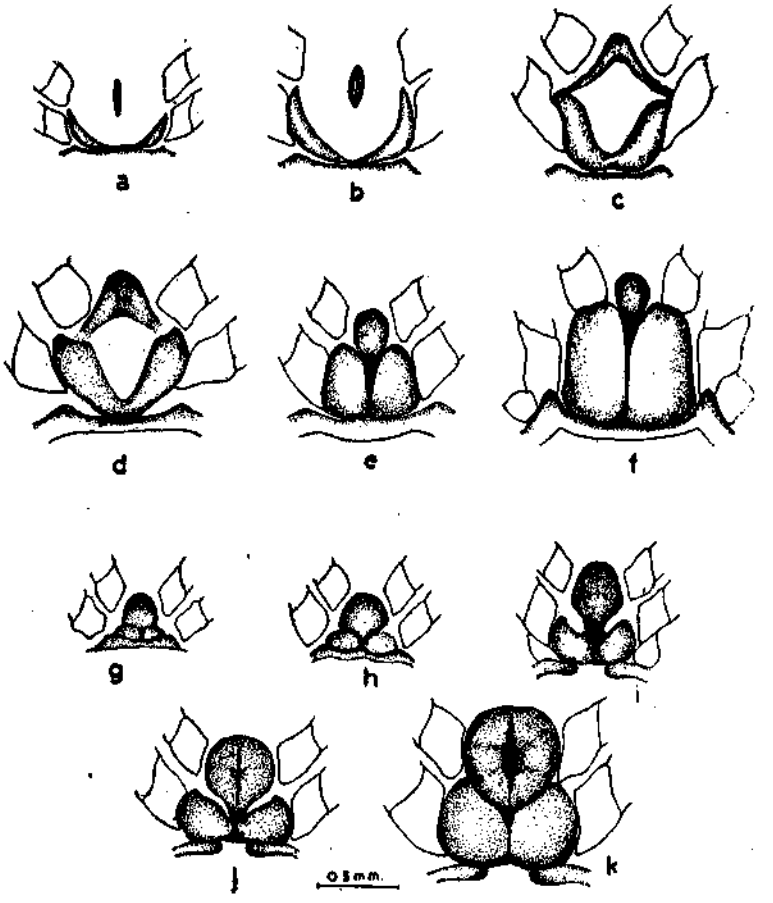

FIG. 2—Development of thelycum of *Penaeus indicus* (a-f) and *Parapenaeopsis stylifera* (g-k). *a*. 35 mm, *b*. 40 mm, *c*. 45 mm, *d*. 55 mm, *e*. 68 mm, *f*. 90 mm, *g*. 24 mm, *h*. 34 mm, *i*. 38 mm, *j*. 45 mm, *k*. 60 mm.

apex. The sides of this raised plate diverge laterally in between the 4th and 5th pereopods. The lateral plates become broader leaving a wide gap between them. When the animal attains 55 mm. size (Fig. 2, d) the median plate gets further raised and this plate at this stage is provided with a median ridge. The lateral plates become broader and extend anteriorly overlapping the lateral sides of the median plate. The anterolateral margin of the lateral plate is slightly indented giving a

bilobed appearance. In the 68 mm. size the anterior region of the median plate gets more rounded (Fig. 2, e). The posterior part of the median plate gets covered over by the two lateral plates which at this stage broadens out considerably, especially the posterior region leaving only a narrow V-shaped gap between the two halves. At 90 mm. size (Fig. 2, f) the lateral plates expand further up filling the V-shaped gap and thereafter gradually the adult characters are reached mostly by further growth in size of the plates.

In the adult thelycum, the median plate is relatively small, anteriorly semicircular in shape and with a pair of lateral processes which are covered over by the anterior part of the lateral plates. From the semicircular portion of the median plate there is a median fleshy and thin process extending posteriorly in between the lateral plates to $\frac{1}{4}$ their length. The two lateral plates occupy the entire space of the sternite in between the 5th pair of pereopods. The lateral plates are broader posteriorly and meet each other in the median line, where the edges of the plates curve upwards. The inner surface of these upcurved edges is fleshy and has a lamellated appearance.

Metapenaeus monoceros

Petasma : In young specimens of 25 mm body length the petasmal endopodites are small, finger-like, nonsetose and measure 0.225 mm (Fig. 3, a). At 30 mm size the length of the endopodite increases to 0.875 mm. and the tip is slightly emarginated. In specimens measuring 35 mm in total length the endopodites measure 1.3 mm (Fig. 3, b). Each half is subrectangular in outline and distally provided with simple inner and outer projections representing the median and lateral lobes. The two lobes are differentiated proximally also by a faint ridge extending up to the middle. The proximal margin of the lateral lobe folds slightly inwards marking the division of the lateral lobe into dorsal and ventral lobules. A slight projection marking the beginning of the posterior projection on the median lobe is developed posteriorly.

At next size (45 mm), the inner apical projection is slightly elongated with the tip more acutely pointed than the outer projection (Fig. 3, c). The length of the lateral fold increases distally to form an open groove. The ridge separating the median and lateral lobes extends up to the distal end. The petasma at this size measures 2.6 mm in length. In specimens measuring 65 mm size (Fig. 3, d) the lateral fold has completely developed, thus forming the dorsal and ventral lobules of the lateral lobes. The length increases to 3.5 mm and there are no hooks discernible on the inner median border. In a 71 mm prawn (Fig. 3; e) the petasma shows considerable modification from the preceding stage. The apical projections fold inwards and the tip of the lateral lobe is more acute than that of the median. A few hooks develop on the inner subterminal median border and near the median proximal border, but the two halves are not united together. Fusion of the two halves of the petasma in fifty per cent of the specimens was found to be at 74.0 mm length (Fig. 9).

In the next size (80 mm.), the hooks are developed all along the median border. The inward fold at the distal end of the median lobe becomes enlarged. The proximal region of this enlarged tip remains narrow and stalk-like. The remaining part gets much broader and bulbous in shape with the tip constricted, twisted and with an orifice laterally. This whole structure looks like a hood overlying the trough-like anterior region of the lateral lobes, the distal margin of which has now three

elevations. These elevations are slightly folded inwards and the outermost projection is the longest with more acute tip. At 105 mm (Fig. 3, f & g) size, the petasma attains all the adult characters and thereafter the growth is in size.

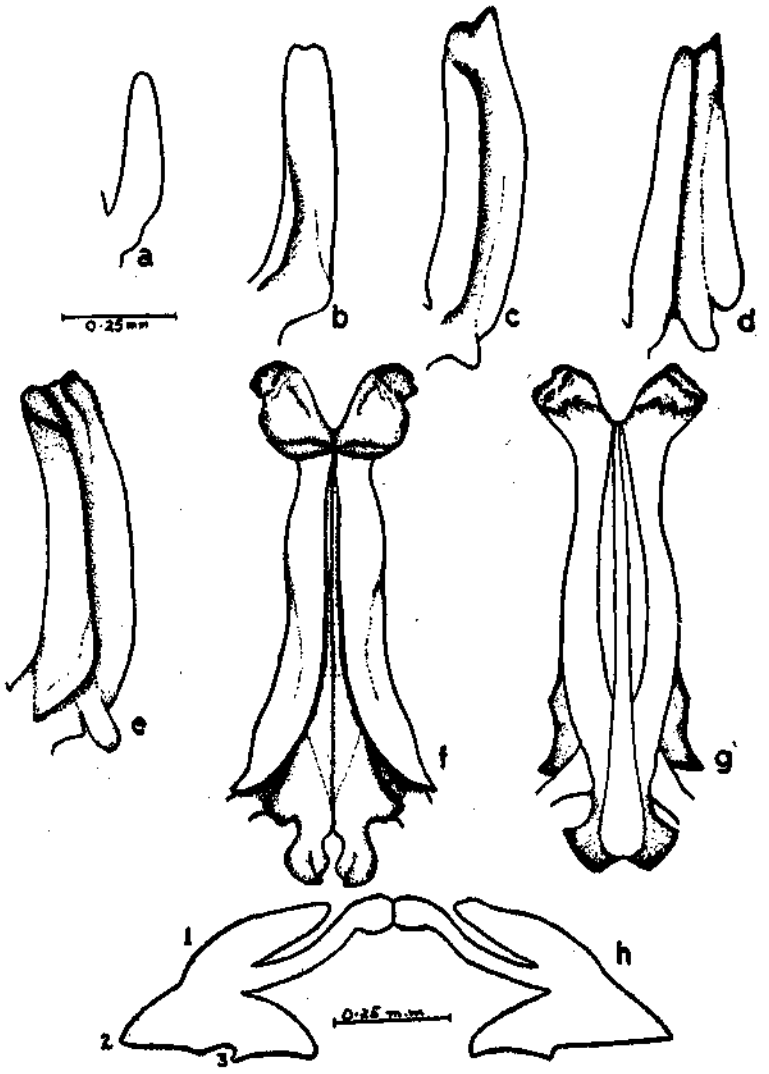

FIG. 3—Development of petasmal endopodites of *Metapenaeus monoceros*. *a*. 25 mm, *b*. 35 mm, *c*. 45 mm. *d*. 65 mm, *e*. 71 mm, *f*. 105 mm, ventral view, *g*. 105 mm, dorsal view, *h*. Cross section of adult petasma (1, 2 and 3 are ridges).

In cross section (Fig. 3, h) the median lobe is thicker than that of *P. indicus* and the lateral lobe much thicker than the median one. Ventral lobules of the lateral lobe are thick and strongly turned medially and extend almost to the median line. Three ridges are present on this lobule (Fig. 3, h-1, 2 & 3). Of these ridges, the third one situated at the anterior surface near the ventral rim of the lobule is

much smaller than the other two. In general feature, the petasma is considerably depressed, subrectangular in outline and almost 3 times as long as wide. The lateral lobes are much thicker than the median lobes and well calcified. As described by Alcock (1906) the median lobe is distally produced into a large gargoyle. The lateral lobes end in 3 projections masked by the hood-like projections of the median lobes on the ventral side. The dorsal lobule of the median lobe is produced posteriorly into a prominent projection with rounded apex. On both sides of these projections the posterior margin is raised into well calcified triangular projections. The lateral sides are well calcified, the posterior edge of which gently curves up sidewise.

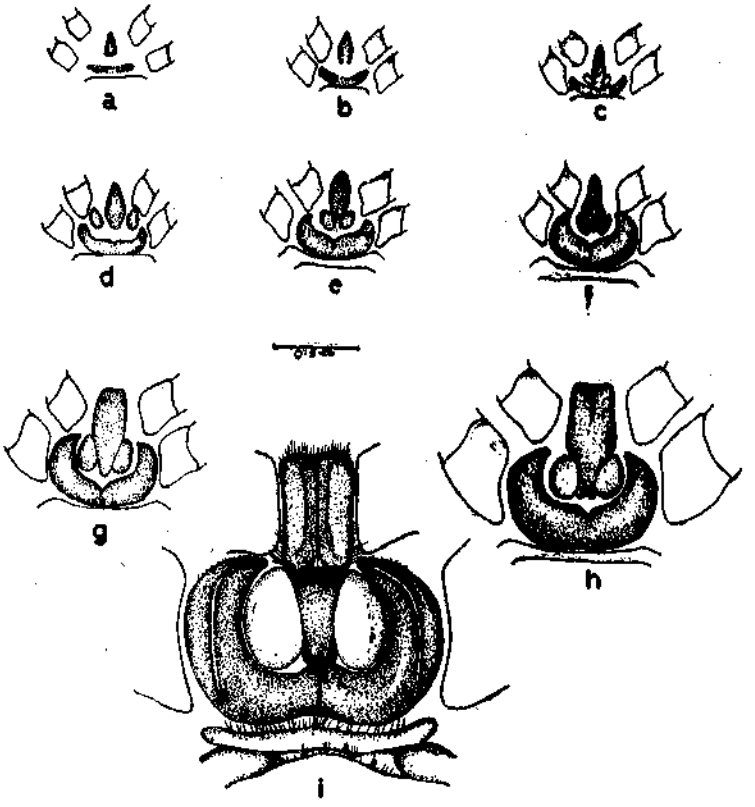

FIG. 4—Development of thelycum of *Metapenaeus monoceros*. *a*. 27 mm, *b*. 30 mm, *c*. 35 mm, *d*. 40 mm, *e*. 45 mm, *f*. 50 mm, *g*. 60 mm, *h*. 82 mm, *i*. adult.

Thelycum : The thelycum of juveniles of 27 mm body length (Fig. 4, a) is differentiated into a small anterior median longitudinal swelling on 7th thoracic sternite and a transverse narrow ridge representing the rudiment of the lateral plates on the next somite. In a specimen of 30 mm. size (Fig. 4, b) these median and posterior ridges are slightly more developed. At 35 mm size (Fig. 4, c) an additional pair of small swellings are developed at the posterolateral sides of the median ridge, one on each side. The lateral plates slowly begin to be differentiated as the two lateral tips develop upward curvature.

At 40 mm. size (Fig. 4, d) the median plate is fairly well developed and there are two oval bosses on its posterolateral sides. The lateral plates further extend anterolaterally and the two plates are fairly distinct. When the prawn grows to 45 mm size (Fig. 4, e) the lateral edges of the median plate gets slightly raised up so that it becomes medially concave. The lateral plates extend further anterolaterally. In a specimen of 50 mm size (Fig. 4, f) the concave median region of the median plate is quite distinct. The lateral plates become broader at the posterior region and the anterolateral tips extend anteriorly partly enclosing the two oval plates situated at the posterolateral sides of the median plate.

At 60 mm. body length (Fig. 4, g) the posterior region of the median plate gets narrower and begins to dip down forming a concave region behind along with the two oval plates. The lateral plates expand further to enclose the oval plates. At 82 mm size (Fig. 4, h) the thelycum attains most of the features of the adult. The tip of the lateral plates now almost reach the sides of the median plate, completely enclosing the posterior portion of the median plate as well as the oval plates in the concave region. The two lateral edges of the lateral plates get raised up to form the typical ear-shaped structure of the adult thelycum. The median plate has a distinct median groove. After this size, the development of the thelycum is mostly in size of the plates.

The adult thelycum (Fig. 4, i) has a concave central region bounded anteriorly by the median plate, laterally and posteriorly by the lateral plates and dorsally by the posterior hollowed out region of the median plate, the two oval plates on the sides of these and the anterior hollowed out regions of the lateral plates. The lateral ridges of the lateral plates are considerably raised to form an ear-shaped structure. The anterior edge of this ridge possesses sparsely set small setae. The anterior half of the median plate is broader and has a distinct groove medially. The posterior half is narrower and descends down forming part of the roof of the concave portion, the posterior tip ending in two slightly elevated knobs. The portion of the concave region between this posterior part of the median plate and the lateral plates is occupied by the two oval plates. The anterior margin of the median plate is beset with setae. The lateral sides of the same also possess setae especially the middle region. The coxae of the 4th pereopods have a sharp vertical ridge which is in close approximation with the sides of the median plate. The posterior ridge of the last thoracic sternite is beset with long setae.

Metapenaeus affinis

Petasma : The development of the petasma in this species shows considerable similarity with that of *M. monoceros*, the main difference being in the development of the distal projections of the lobes. In a specimen of 32 mm. size, the petasmal endopodite is finger-like (Fig. 5, a). It measures 0.75 mm. in length. Near the proximal inner margin is a small constriction followed anteriorly by a small knob which is the rudiment of the developing posterior projection of the petasma. At a length of 42 mm., the endopodite increases in size to 1.5 mm. and it is 5.5 times as long as wide. At the tip, the margin is slightly indented to form small apical projections. The median lobe as well as the lateral fold of the lateral lobe are defined in proximal one-fourth distance. The posterior protuberance is further extended with rounded margin. The petasma of specimens 45 mm. long (Fig. 5, b), measures 1.8 mm. At this stage, the apical projections are simple and well developed. The lateral folding extends further anteriorly and the ridge separating the median and lateral lobes extends to the tip.

In 55 mm specimens (Fig. 5, c) the size of the endopodite increases to 2.3 mm An additional knob-like projection develops on the lateral side of the posterior projection and also the lateral fold extends to the tip. In the following size examined (65 mm), the lateral apical projection folds inwards and the lateral longitudinal fold forms an open groove, (Fig. 5, d). The inner apical projection remains simple. Even though, the two halves of the petasma remain apart, a few hooks develop at the inner subterminal median border. The length of the endopodite at this stage is 2.8 mm. As the prawn attains 70 mm size, the inner apical projection also gets

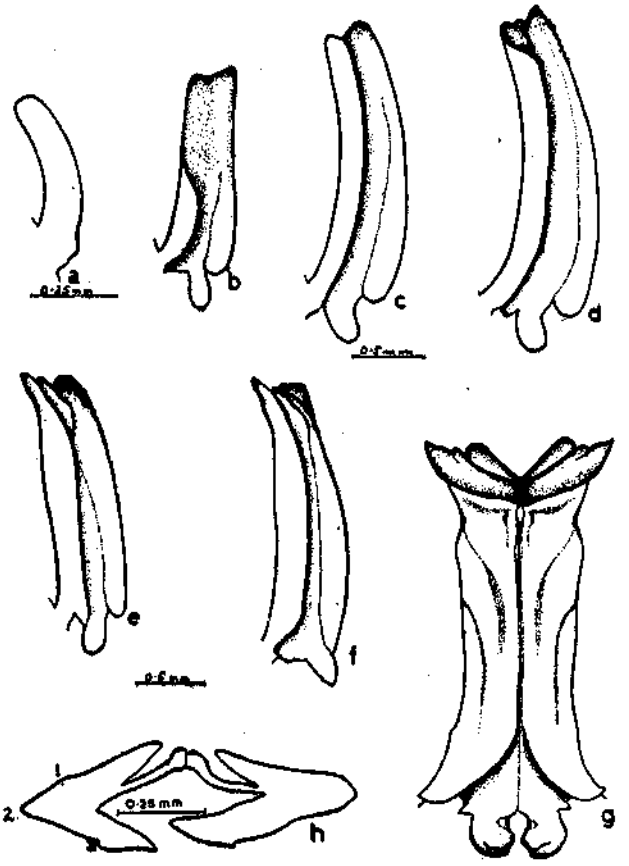

FIG. 5—Development of petasmal endopodite of *Metapenaeus affinis*. *a*. 32 mm, *b*. 45 mm, *c*. 55 mm. *d*. 65 mm. *e*. 70 mm, *f*. 80 mm, *g*. 120 mm, *h*. Cross section of adult petasma (1, 2 and 3 are ridges).

folded inwards and the lateral projection develops an additional smaller elevation with the tip lightly folding inward, just inside the first fold which now is much larger in size and directed laterally (Fig. 5, e). More hooks are developed on the median line, but the petasmal endopodites are still unjointed. The size of the endopodite now is 3.0 mm. In specimens measuring 80 mm (Fig. 5, f) the petasmal endopodite attains 4.0 mm in length and develops hooks all along the median margin. From Fig. 9 the size at which fifty per cent of the prawns had the petasmal endopodites fused was found to be 71.6 mm length.

At 90 mm size, the tip of the middle lobe increases in size and partly covers the apical folds of the lateral lobes. The two halves are united by means of the hooks and the petasma has almost all the characters of that of the adult. Thereafter there is only increase in size.

In cross section (Fig. 5, h) although it is quite similar to *M. monoceros* the median lobe is slightly thinner. In general feature, the important difference from *M. monoceros* is in the nature of the distal projections of the different lobes. The distal ends of the ventral as well as dorsal lobules of the lateral lobe are produced distolaterally into horn-like projections, that of the ventral lobules being larger in size. The median lobe is distally expanded into a rounded fold which partly covers the distolateral projections of the lateral lobes. The distal end of the petasma thus ends in a pair of two-lipped spouts which look like a pair of short horns as described by Alcock (1906).

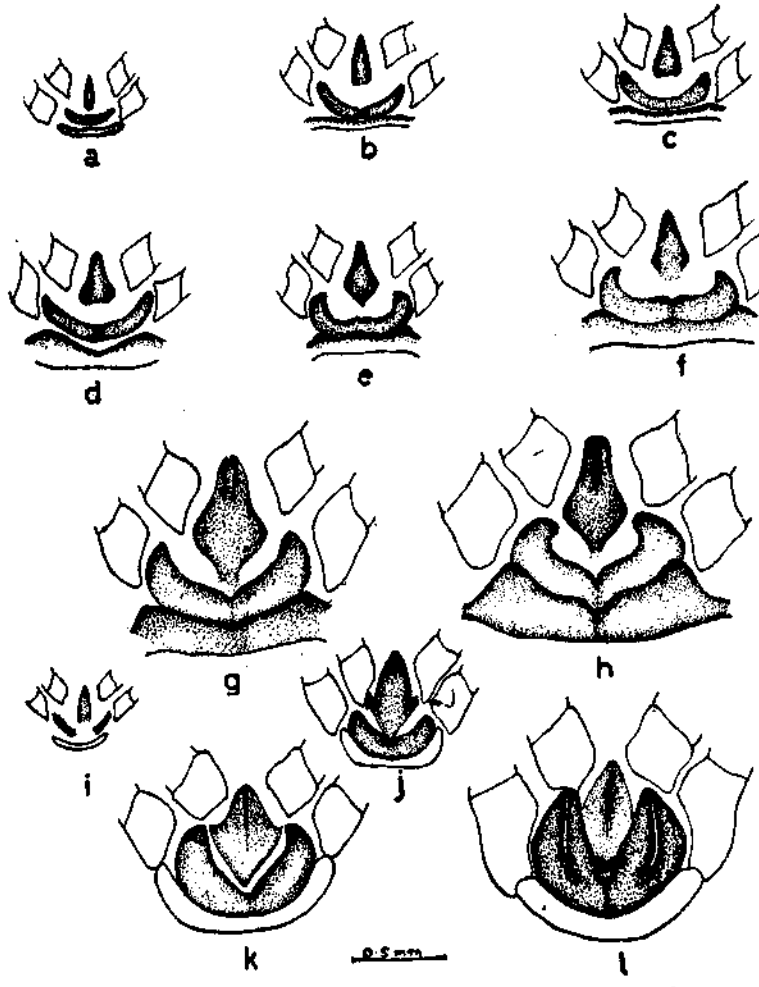

FIG. 6—Development of thelycum of *Metapenaeus affinis* (a-h) and *Metapenaeus dobsoni* (i-l). *a*. 31 mm, *b*. 36 mm, *c*. 40 mm, *d*. 45 mm, *e*. 51 mm, *f*. 58 mm, *g*. 65 mm, *h*. 75 mm, *i*. 20 mm, *j*. 45 mm, *k*. 51 mm, *l*. 65 mm.

Thelycum : The development of the thelycum in this species, although follows the same pattern as in *M. monoceros*, shows some important differences from the same. In a 31 mm body length prawn (Fig. 6, a) the thelycum is already differentiated by a small anterior median longitudinal ridge between the 4th pereopods and a horizontal narrow swelling in between the 5th pereopods. In a 36 mm size specimen the median ridge is larger and the posterior plate gets differentiated into two halves forming the rudiments of the lateral plates (Fig. 6, b). Posterior to these lateral plates, is the posterior ridge of the rearmost thoracic sternite. At 40 mm body length (Fig. 6, c) the median ridge gets further extended and broader posteriorly and the lateral plates extend anteriorly giving a concave appearance to the plates. In the next size (45 mm) the median plate develops a faint groove with the development of raised ridges at the lateral edges. The lateral plates are noticed extending and curving further anteriorly (Fig. 6, d). The important development at this stage is the appearance of two convex upheavals, one on each side posterior to the lateral plates, from the posterior ridge of the rearmost thoracic sternite. In a 51 mm size specimen (Fig. 6, e) the median plate and the lateral plates attain their characteristic shapes and the two swellings from the posterior ridge of the rearmost thoracic sternite gets further extended anteriorly, almost reaching the posterior margin of the lateral plates.

At 58 mm. size (Fig. 6, f) the groove in the median plate is quite distinct and tips of the lateral plates are well curved up, reaching near the posterior part of the median plate. The plates extending from the posterior ridge of the last thoracic sternite extend and almost overlap the posterior margin of the lateral plate. At 65 mm length (Fig. 6, g) the thelycum is similar to that of the previous stage, except, for the increase in size of the different plates. In 75 mm specimen, the thelycum shows most of the characteristics of the adult (Fig. 6, h). The median plate has conspicuous groove medially. Posteriorly this plate gets narrower and descends down. The lateral plates have the typical adult shape, extending to the widest region of the median plate at $\frac{1}{4}$ its length from the posterior end. The plates developed from the posterior ridge of the last thoracic sternite are quite conspicuous and appear as the posterior half of the lateral plates. Thereafter, the thelycum increases in size of the plates and along with the appearance of setae acquires adult characters.

The adult thelycum consists of an anterior median plate and the lateral plates situated on 7th and 8th thoracic sternites respectively. The median plate is narrower anteriorly with the maximum width at $\frac{3}{4}$ length. From this broadest region it becomes narrow and descends down up to the anterior concave median margin of the lateral plates. The anterior half of this plate has a median groove. The lateral plates are flattish without the ear-shaped raised edges of *M. monoceros*. These are transversely cut into two unequal segments, the posterior appearing as overlapping the anterior segments which are broad and flat with their anterolateral tips curving up and almost reaching the lateral sides of the broadest portion of the median plate. Setae are present at the anterior margin and also the posterior narrower region of the median plate. A few setae are also present at the margins separating the two segments of the lateral plates.

Metapenaeus dobsoni

Petasma : The development of the petasma of this species has been partly described by Menon (1951). According to him, the petasma makes its appearance

as a thin foliaceous process at the late postlarval stage of slightly over 15 mm size. However, the present study shows that the bud-like rudiment of the petasmal endopodite appears at a length of 12 mm (Fig. 7, a). At this size, it is a small, blunt projection measuring 0.05 mm in length, carrying an apical hair. At 15 mm size (Fig. 7, c) the endopodite increases in size to 0.125 mm and at 19 mm size it measures 0.3 mm. (Fig. 7, d). Now it is finger-like and the apical hair is comparatively smaller than that of the previous stages. At the proximal inner margin a small elevation is developed which is the rudiment of the posterior projection of the adult petasma. When the animal attains 24 mm size (Fig. 7, e), the endopodite is still finger-like but devoid of the apical seta and the size is 0.525 mm. A faint ridge demarcating the median and lateral lobes is visible medially. The presence of the apical seta has not been recorded by Menon (*op. cit.*) at any stage. At 30 mm. length the finger-like shape disappears (Fig. 7, f). It is more elongated and distally two projections are visible. The lateral margin folds inwards forming a complete fold representing the ventral lobule of the lateral lobe. Proximally, the median lobe is angular and the posterior projection is fairly developed with rounded apex. The petasma at this stage measures 1.25 to 1.5 mm in length. As the prawn grows to 42 mm, important changes noticed are at the distal ends (Fig. 7, g). The apical pro-

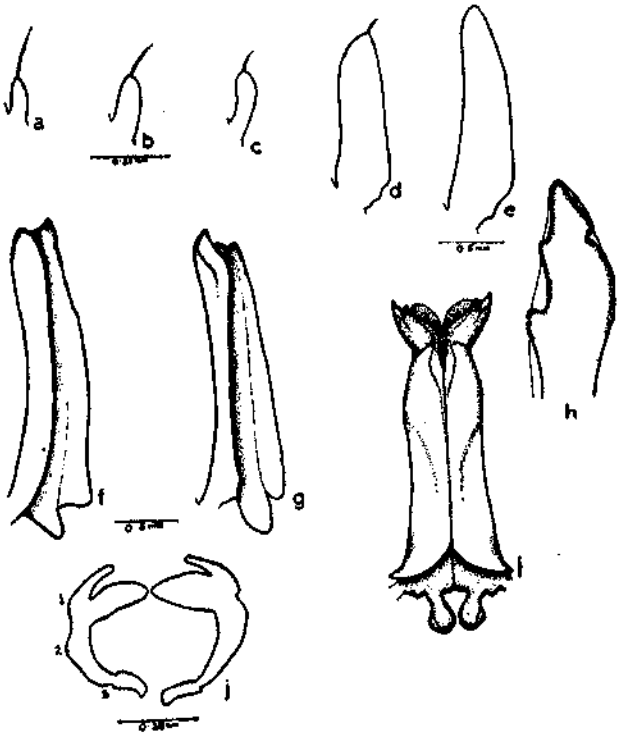

FIG 7—Development of petasmal endopodite of *Metapenaeus dobsoni*. *a*. 12 mm, *b*. 14 mm, *c*. 15 mm, *d*. 19 mm, *e*. 24 mm, *f*. 30 mm, *g*. 42 mm. *h*. 55 mm, lateral view, *i*. 65 mm, *j*. Cross section of adult petasma (1, 2 and 3 are ridges).

jection of the ventral lobule of the lateral lobe gets enlarged and elongated with an inward curve. A smaller projection is developed at the tip of the dorsal lobule of the lateral lobe. The median lobe remains simple apically. Hooks are developed

in the median border at the subterminal and proximal regions. The length at this stage is 2.1 mm.

In the next size (55 mm) considerable changes occur at the tip. The tip of the median lobe gets rounded and fleshy with the surface having a corrugated appearance. Tubercles are also present on this surface. The lateral projection of the lateral lobe is more elongated distally and with acute tip. Proximally, the posterior projection gets more rounded and the lateral margin curve upwards. Hooks are developed all along the median margin of each endopodite so that the fusion of the two halves of the petasma takes place at more or less this size. The size at which fifty per cent of the specimens were with fused endopodites as indicated by Fig. 9 is 53.6 mm. On the dorsal side of each endopodite a pair of blunt triangular projections are present on the anterior half of the median lobe (Fig. 7, h). The anterior smaller one is situated behind the tip and the other pair slightly posterior to that. After this stage the development of the petasma is a matter of growth in size and calcification of some of the lobes and margins.

Compared to *M. monoceros* and *M. affinis* this species shows some difference in the cross section, although belonging to the same type. The median lobe is very much thicker (Fig. 7, j). The ridge at the median line of the outer surface of the lateral lobule (2 in fig.) is not very prominent. In general feature also the adult petasma shows some differences from the preceding species. Median lobe is considerably thick and fleshy. Distally the petasma ends in a pair of spouts. The tip of the lateral lobe is prolonged distolaterally with acute tip. The distal tips of the median lobes are also produced distomedially into a fleshy spout-like structure with corrugated surface and provided with tubercles. A few tubercles are also present on the distolateral spouts on the lateral surface. Ventrally, inner to the distomedian lobes is a pair of thick stumpy curved filaments which are hidden completely in the dorsal view (Fig. 7, i). On the dorsal surface, just at the base of the spouts is situated a pair of papillae with pointed tips which are curved ventrally. Posterior to this there is another pair of triangular plates originating from the median lobes with the extremities provided with a wavy margin put in apposition to one another. The lateral edges of the petasma is well calcified and posteriorly curved up. The posterior projection is well calcified and similar to that of the other species.

Thelycum : The development of the thelycum of this species has been partly described by Menon (*op. cit.*). He has described the development from 25 mm size onwards. Specimens of smaller sizes were found to have the thelycum differentiated. At 20 mm size (Fig. 6, i) there is a median elongated ridge on the 7th thoracic sternite and a pair of small obliquely placed transverse ridges posterior to this. The ' crescentic groove ' referred to by Menon (*op. cit.*) runs in between the anterior and posterior ridges. Behind this, the posteriormost thoracic sternite develops a faint transverse ridge. Further development has been traced by Menon (*op. cit.*) and only the additional features noticed are mentioned here. At 45 mm size the median ridge has attained the form of an elongated oval plate with the anterior and posterior ends narrow. The lateral margins at the broader middle region diverge to short ridges as shown in Fig. 6, j. The lateral plates have become broader and the anterolateral tips curve upwards reducing the gap between it and the posterolateral border of the median plate. In the next size (51 mm) the anterior region of the median plate develops a faint median groove (Fig. 6, k) and the lateral plates extend further anteriorly almost reaching the widest region of the median plate

and attain the characteristic horse-shoe shape. A faint ridge is noticed medially on the lateral plates. At 65 mm body length (Fig. 6, l) the thelycum attains most of the adult characters. The lateral plates grow further and overlaps the lateral portions of the posterior part of the median plate including the lateral ridges. The median ridges on the lateral plates are now well developed and conspicuous. The anterior exposed portion of the median plate remains tongue-shaped with a median shallow groove. In later sizes, the different plates increase in size and the posterior median margin of the lateral plates almost come together at the median line.

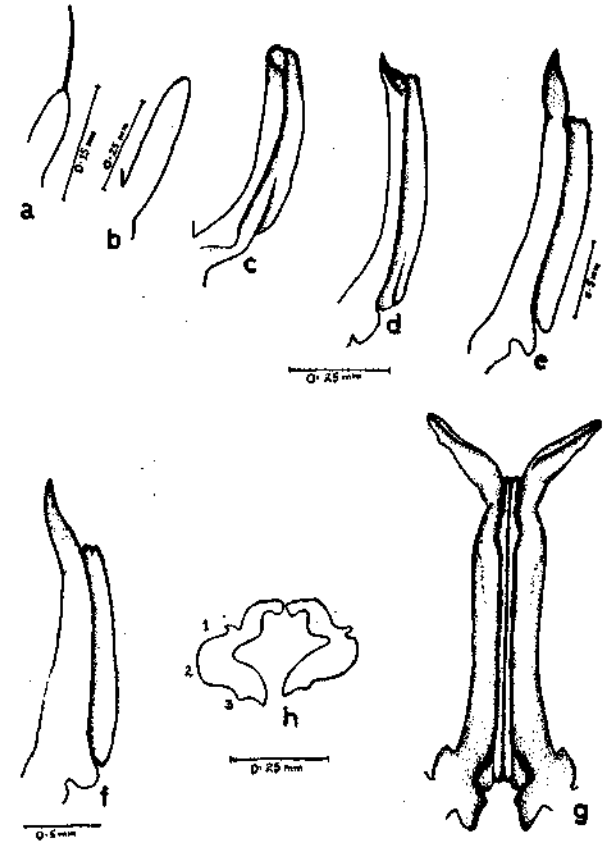

FIG. 8—Development of petasmal endopodite of *Parapenaeopsis stylifera*. *a*. 18 mm, *b*. 25 mm, *c*. 35 mm, *d*. 40 mm, *e*. 48 mm, *f*. 56 mm, *g*. adult, *h*. Cross section of adult petasma (1, 2 and 3 are ridges).

The adult thelycum has a median plate situated on the 7th thoracic sternite and is broadest in the middle tapering anteriorly to a narrow rounded tip. The posterior half of this plate is partly overlapped by the lateral margins of the lateral plates. These lateral plates are situated on 8th thoracic sternite and together appear horse-shoe-shaped. Each plate is with a median ridge which extends almost the entire length of the plate.

Parapenaeopsis stylifera

Petasma : In a juvenile specimen measuring 18 mm in body length (Fig. 8, a) the petasmal endopodite has developed as a small bud-like projection with an apical seta and it measures 0.075 mm. At 25 mm size (Fig. 8, b) the apical seta disappears and it is elongated and finger-like measuring 0.375 mm. In specimen measuring 35 mm the endopodite shows considerable development and measures 0.825 mm in length (Fig. 8, c). The outer lateral margin folds inwards and a ridge is developed separating the median and lateral lobes of the petasma and this is evident at the tip also by the indentation at the margin. Posteriorly the lateral lobe develops a small projection. As the prawn grows to 40 mm in size (Fig. 8, d) the petasma measures 1.05 mm and the lateral fold has completely developed. The distal tip of the outer lobe gets elongated with narrow and pointed tip. The median lobe remains almost the same as in previous stage. At 48 mm length (Fig. 8, e), the anterior tip of the lateral lobe is further elongated and directed anterolaterally. The inner median border of the endopodite develops a few hooks at the anterior region. The posterior projection of the lateral lobe is now well developed with rounded tip. At 56 mm size, the petasma measures 2.75 mm and has attained most of the adult characters (Fig. 8, f). The inner median border develops more hooks so that the two halves are partly fused. The anterolateral projection of the lateral lobe is well developed with pointed tip. Thereafter the growth takes place in size only. Although the hooks are developed along the median margin of the endopodite at 46-50 mm size, the data summarised in Fig. 9 shows that the size at which fifty per cent of the prawns had fused endopodites was 59.0 mm.

In cross section, the adult petasma has the median lobe similar in thickness to that of *M. monoceros* and *M. affinis* (Fig. 8, h). The lateral lobe is thicker than the median lobe. The ventral lobules of the lateral lobe are strongly turned medially so that the ventral free tips almost come together in the middle. Ridge at the boundary between the dorsal and ventral lobules (1 in Fig.) is small in comparison with the preceding species of *Metapenaeus*.

In general feature, the petasma is somewhat narrow distally. Median lobe is small and without the posterior projection which is present on the lateral lobe. The ventral lobule of the lateral lobe is calcified and distolaterally produced into a long tubular process. About $\frac{1}{4}$ distance from the tip of this process there is a small notch.

Thelycum : In a young prawn measuring 24 mm in length, the rudiments of the thelycal components are fairly well differentiated (Fig. 2, g). A median semicircular plate situated on the penultimate thoracic sternite, a pair of small swellings immediately behind it and a transverse plate in the last thoracic sternite are visible. When the prawn grows to 34 mm size, the anterior median plate slightly increases in size and it is now broader than long (Fig. 2, h). The swellings of the two posterior plates are more conspicuous. At 38 mm size (Fig. 2, i) the anterior portion of the median plate remains almost the same, but the posterior region gets narrower and extends backwards. The anterolateral margins of the posterior plates extend upward along the sides of the posterolateral margin of the median plate. In the next size (45 mm), the anterior portion of the median plate appears semicircular (Fig. 2, j) and the narrow posterior portion develops a boss-like projection which occupies the median concave depression formed by the anterolateral extension of the anterior margins of the posterior plates. At 60 mm size (Fig. 2, k) the thelycum has most of the adult characters and afterwards as the growth progresses the thelycal plates increase in size.

The adult thelycum of the species consists of a median anterior plate and two lateral plates. The median plate is broad and squarish, beset with setae at the anterior border and posteriorly produced into a short stalk which fits into the

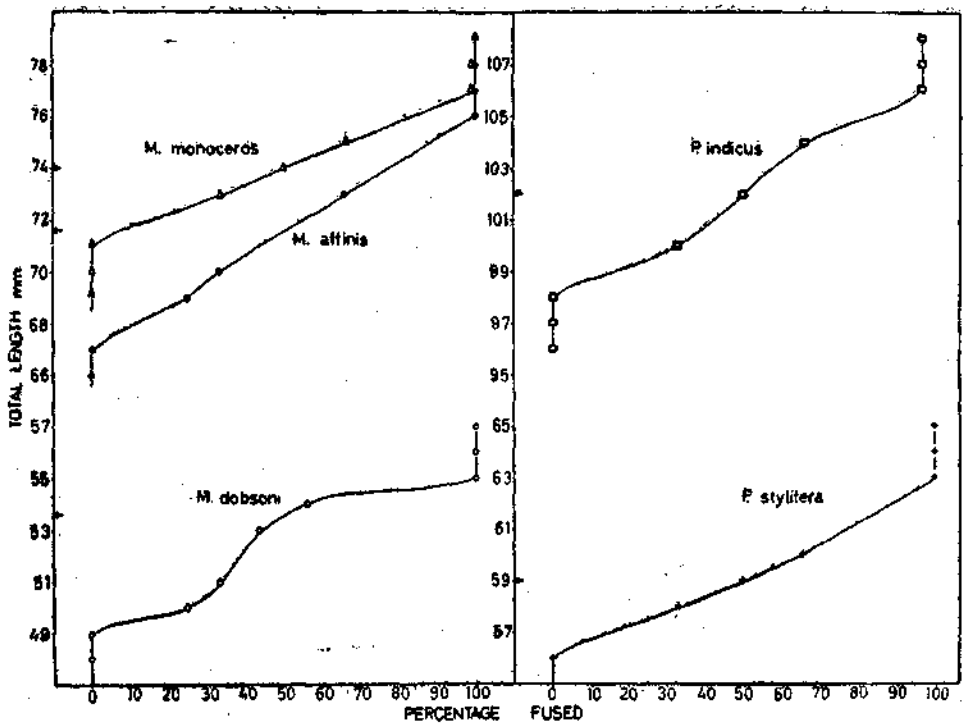

FIG. 9—The size of males at which the petasmal endopodites fuse together.

anteromedian indentation of the posterior plates. The lateral plates are fused at the posterior margin and bifid anteriorly into the gap of which fits in the posterior stalk of the median plate.

GENERAL REMARKS

Although the adult petasma of penaeids is a complex organ, it develops initially as a small bud-like projection on the first pleopods. But, the shapes of the different lobes constituting the organ and the disposition of the distal projections in the developing and adult petasmata of the different species vary considerably. A comparison of the development of petasma among the five species dealt with reveals that *P. indicus* has a simple pattern of development, while the species of *Metapenaeus* and *P. stylifera* demonstrate slightly specialised condition. In *P. indicus* the median lobes especially the tips are not much modified, in which character the petasma of *P. stylifera* is similar. In all the species of *Metapenaeus* under study the distal extremities of the median lobes are well developed and greatly modified, generally overlying the trough-like anterolaterally directed ends of the lateral lobes. In the case of *P. indicus* the tips of the lateral lobes are curved inwards, while in *P. stylifera* these are elongated anterolaterally. *M. dobsoni* differs from other

species in having a pair of triangular calcified projection on the anterior median dorsal region (vide supra) providing an additional attachment to the two halves of the petasma. The posterior rounded projections on the median lobes of the species of *Metapenaeus* and *P. indicus* are conspicuously absent in *P. stylifera*, in which case smaller projections are present on the lateral lobes posteriorly.

In early development *P. indicus* differs from *P. monodon* and *P. semisulcatus* described by Kubo (*op. cit.*) in the absence of an apical seta and bristle at $\frac{1}{3}$ distance from the inner proximal margin of the developing petasmal endopodites. Further, the distolateral spine observed in the endopodite of *P. monodon* at about 55 mm. size by Kubo is not noticed in *P. indicus*. The presence of an apical hair on the endopodite in the very early sizes is a feature noticed in *M. dobsoni* as well as *P. stylifera*.

The development of the thelycum in all the species follows more or less a similar pattern, originating as a median ridge and two posterior swellings representing the median and two posterior plates respectively. In *M. monoceros*, however, there is an additional pair of swellings posterolaterally to the median ridge, developing into a pair of additional oval plates. In structure, the thelycum of *P. indicus* differs from other species in that the median plate is much smaller than the posterior plates. Menon (1951) is of opinion that the median thelycal plate of *M. dobsoni* is developed from the median spine on 7th thoracic sternite present in the early postlarva. However, from the present study it is not possible to establish clearly that this plate is formed by the enlargement of this spine. It can only be said that the median plate develops at a place where the spine was situated in the early postlarvae. Kubo (*op. cit.*) observes that the median plate does not originate from the sternal spine of the 7th thoracic somite in *Metapenaeus* spp.

A comparative study of the structural development and the general configuration of both petasma and thelycum of these species throws some light on their phyletic relationship. Taking into consideration the simplicity of development and primitive characters like membraneous nature of the different lobes, the absence of longitudinal folds, simple nature of the distal projections of petasma and the simple nature of the posterior plates of the thelycum, it appears that among the five species under study *P. indicus* is more primitive. *P. stylifera* shows slightly more advanced condition, while the three species of *Metapenaeus* occupy a higher position. Among the latter, the simplest form of petasma and thelycum is met with in *M. dobsoni*, whereas, *M. monoceros* shows highly modified distal projection of the petasma and an additional pair of plates in the thelycum. This is quite in agreement with the intergeneric phyletic relationship of penaeids drawn by Kubo (*op. cit.*).

Since all the species except *P. stylifera*, included in the present study are found in different environments, spending their juvenile life in estuaries and adult life in the sea, the influence of these environments on the development of external genitalia is worth consideration. From a study of the size frequencies of the different species of prawns caught from the backwaters and the sizes in which the major developments of the genitalia take place in the respective species, it is clear that almost the entire developmental phase of these organs is during the estuarine phase of the life of the prawns. In the case of *P. indicus*, George (1962b) observes that after about 110-120 mm. length is attained in Cochin backwaters migration back to the sea takes place. The development of both petasma and thelycum traced earlier clearly indicate that when this size is reached, both genitalia have acquired most

of the characters of the adult and the development thereafter is mostly in size of the organs, appearance of setae etc. In the case of other prawns also the sizes recorded for migrating back to the sea from estuarine environment (Menon, 1955 ; George, 1959, 1962a) are at a length when most of the developmental changes in the genitalia are over. These in addition to the fact that no specimens are obtained in the estuarine environment at any time with mature gonads would suggest that although the prawns are almost ready for maturing as indicated by the nature of the external genitalia, some changes in the metabolism of these prawns should trigger further maturation and subsequent spawning and that appear to be happening only in the sea. Probably, the environmental factors like higher salinity, lower temperature or greater pressure of the deeper water of the sea may have some important part to play in this phenomenon.

Acknowledgements

The authors are grateful to Dr. S. Jones for the interest shown during the progress of this work and to Dr. R. Raghu Prasad and Shri K. H. Mohamed for critical reading of the manuscript.

Summary

The development of the external genital organs of five commercially important penaeid prawns of India has been traced from early stages to adult form. The development of these organs in *Penaeus indicus* follows a simple pattern, while that of *Parapenaeopsis stylifera* and all the species of *Metapenaeus* exhibit increasingly specialised condition in the presence of well developed longitudinal folds as well as conspicuously modified distal projections in the petasma and the nature of the different plates in the thelycum. The size at which fifty per cent of the males had the petasmal endopodites fused was found to be 102.0 mm in *P. indicus*, 74.0 mm in *M. monoceros*, 71.6 mm in *M. affinis*, 53.6 mm in *M. dobsoni* and 59.0 mm in *P. stylifera*. A comparison of the developmental features of the different species is made and their phyletic position discussed.

References

Alcock, A. 1906. *Catalogue of the Indian Decapod Crustacea in the collection of the Indian Museum. Part III. Macrura. Fasciculus I.* The prawns of the *Penaeus* Group, 1-55.

Bate, C. Spence 1888. Report on the crustacea Macrura collected by H. M. S. Challenger during the years 1873-76. *Report on the Scientific results of the voyage of H. M. S. Challenger during the years* 1873-76. *Zoology*, **24** : 1-942.

Burkenroad, M. D. 1939. Further observations on Penaeidae of the Northern Gulf of Mexico. *Bull. Bingham Oceanogr. Coll.*, 6(6) : 1-62.

Eldred, B. 1958. Observations on the structural development of the genitalia and impregnation of the pink shrimp, *Penaeus duorarum* Burkenroad. *Fla. St. Bd. Conserv. Mar. Lab. Florida. Tech. Ser.* 23 : 1-26.

George, M. J. 1959. Notes on the bionomics of the prawn *Metapenaeus monoceros* (Fabricius). *Indian J. Fish.*, 6(2) : 268-79.

———. 1962a. On the breeding of penaeids and the recruitment of their postlarvae into the backwaters of Cochin. *Ibid.*, Sec. A., 9(1) : 110-16.

GEORGE, M. J. 1962b. Observations on the size groups of *Penaeus indicus* in the commercial catches of different nets from the backwaters of Cochin. *Ibid.*, Sec. A., 9(2) : 468-75.

HALL, D. N. F. 1962. Observations on the taxonomy and biology of some Indo-West Pacific Penaeidae (Crustacea, Decapoda). *Colonial Office Fish. Publ.*, **17** : 1-229.

HELDT, J. H. 1938. La reproduction chez les crustaces decapodes de la famille des Penaeides. *Ann. Inst. Oceanogr. Paris*, **18**(2) : 31-206.

KISHINOUYE, K. 1896. Peculiar copulatory organ of Penaeidae. *Zool. Mag.*, **8**(96).

———. 1898. Copulatory organ of penaeidae. *Ibid.*, **10**(111).

———. 1900. Japanese species of the genus *Penaeus*. *Jour. Fisheries Bur.*, **8**(1) : 1-29.

KUBO, I. 1949. Studies on the Penaeidae of Japanese and its adjacent waters. *J. Tokyo Univ. Fish.*, **36** (1) : 1-467.

MENON, M. K. 1951. The life history and bionomics of an Indian penaeid prawn, *Metapenaeus dobsoni* Miers. *Proc. Indo-Pacif. Fish. Counc.*, 3rd meet, 80-93.

———. 1955. Notes on the bionomics and fishery of the prawn *Metapenaeus dobsoni* Miers on the South-west coast of India. *Indian J. Fish.*, **2** (1) : 41-56.