

## The Moulting Stages of the Pea-Crab (*Pinnotheres pisum*).

By

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With Plates I-V and 4 Figures in the Text.

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*Pinnotheres pisum* is a small crab with a carapace between about 2.1 and 18 mm. wide. The females are commonly found parasitic in the mussel, *Mytilus edulis*, though they have been recorded from other bivalves. The males are free-swimming and are comparatively rarely found in mussels. These small crabs are never abundant, and not more than one female has ever been found in a mussel.

### SEXUAL DIMORPHISM.

It is well known that there is a marked sexual dimorphism in *P. pisum*. This is, no doubt, due to the difference in the mode of life of the two sexes, the male being active and free swimming, while the female is parasitic. Contrary to what usually occurs in the Brachyura, the adult male is much smaller than the adult female. The male has a carapace varying in width between 3.6 and 7.7 mm., while that of the female may reach a size of 18 mm.

### DESCRIPTION OF THE MALE.

Normally the males, young and adult, are of one form (Plate I, Figs. 1 and 2). A few abnormal crabs, however, have been found, and it is hoped to refer to them in a later paper.

The carapace of the male *P. pisum* is almost circular; very strong and hard and for the most part glabrous. It is very light grey or fawn in colour, with a conspicuous pattern of pale yellow areas outlined with darker yellow or yellowish orange. There is a slight variation of the pattern in different males; in the larger crabs the yellow areas increase in size and fuse to cover the greater part of the dorsal surface of the carapace. Lines and areas of colour also occur on the chelipeds and legs, while on the ventral surface are a few, more or less symmetrically placed,

pale yellow spots. There are frequently numerous black, with an occasional red, chromatophores scattered over the body.

The chelipeds (Plate IV, Fig. 15) are hairy; the palms broad and rather swollen. There are two rows of setæ beneath the chela; one reaches from the base of the palm to the tip of the finger, while that which is visible on the inner surface extends only slightly beyond the base of the immovable finger. These two rows are widely apart at the base of the palm, but converge distally. In the longer row the setæ, which point towards the tip of the finger, are stout and curved. A large tooth is present near the base of the dactylus, and fits a slight notch in the propodial finger. This notch has a small tooth at either end. Both biting surfaces bear stiff setæ, and towards the tips of the fingers small, closely set, spines. In some males the small teeth on the propodial finger are absent, as well as the curved spines from both fingers.

The walking-legs (Plate IV, Figs. 17, 19, 21) are strong, somewhat flattened, and exceedingly hairy, the long hairs being plumose. The second and third legs are especially hairy, the three distal segments bearing two thick fringes of very long hairs, one attached on the lower margin and one near the upper margin on the posterior surface. The extreme hairiness of the legs, as well as their flattened form, assists in maintaining a free swimming existence. The second and third legs are subequal in length, the second being slightly the longer. The first leg is the next in length, and the fourth leg the shortest. The short, curved dactyli end in short, horny tips.

The abdomen is narrow and tapering. Two small, transversely ridged, nodules of chitin are present on the fifth thoracic somite, and these fit into two pockets on the sixth segment of the abdomen. By this arrangement the abdomen is securely fastened to the thorax.

The copulatory organs of the male (Text Fig. 1) are large; the first appendage is blade-like and hairy, with the tube, or rather the closed groove, running along its inner side. Numerous rosette glands are present round the lower portion of the groove. The second appendage is rod-like with a swollen base. The distal portion is normally carried within the groove of the first appendage. This stylet, unlike the first, is almost hairless, and is without glands.

#### GROWTH STAGES OF THE FEMALE.

The female occurs under two forms: the young female is almost indistinguishable from the male, while the next and subsequent stages are entirely different in appearance, and are what may be considered typically female in form. This change in form occurring between Stage I and II would appear to be related to the change in the mode of life, though

it would seem that it can only take place after copulation. One exception has been found among the material so far examined; a Stage I female more nearly resembling the female form than the male though with empty spermathecae.

After the typically female form is assumed in Stage II, the further growth stages are mainly a development of those structures connected with reproduction, together with a general increase in size. Somewhat similar growth stages have been described for the female *Haplocarcinus* by Potts (6).

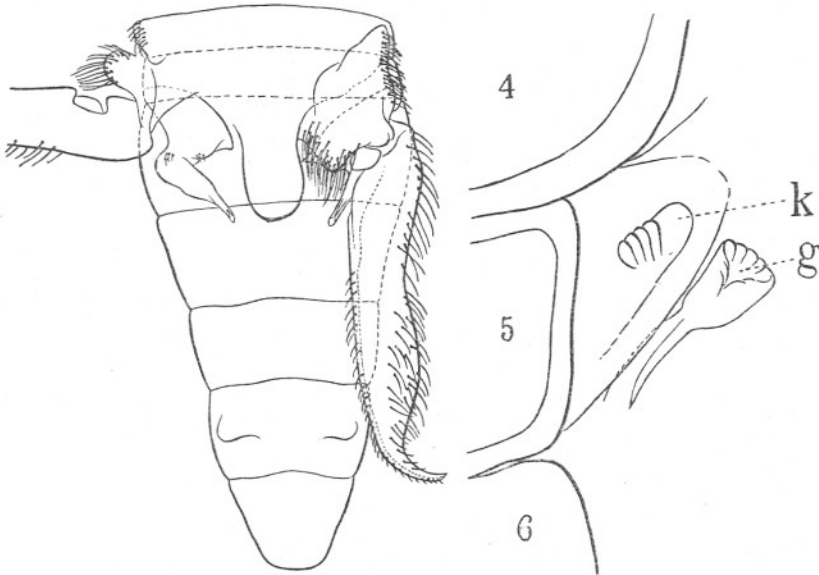


FIG. 1. Male abdomen and copulatory appendages. The first appendage of the right side is turned aside to expose the second appendage. Magnification, ca. 16 $\frac{2}{3}$ .

FIG. 2. Genital aperture and chitinous knob of right side of a Stage I female. g = genital aperture, k = chitinous knob; 4, 5, 6 = 4th, 5th, 6th thoracic somites. Magnification, ca. 71.

The female crab becomes parasitic in the mussel, *Mytilus edulis*. The parasitic life has exerted a considerable influence on the structure of the female, which is modified to a certain extent. It is large and extremely passive; the carapace with the rest of the exoskeleton being no longer needed for protection is soft and membraneous; the eyes are very minute, and in the fully adult crab invisible from the dorsal surface.

As noted by Orton (4) the female only reaches its adult form after passing through a number of growth stages. The greater part of the work recorded in this paper has been to determine these stages. The majority of them have been verified by a series of moults.

*Stage I* (Plate II, Figs. 3, 4). The young Stage I female, which has been found with a carapace varying in width between 2.1 and 4.9 mm., can only be distinguished from the male by the genital openings and the abdominal appendages. Indeed, the resemblance is so close that Orton (4) records that, on obtaining a female form moulted from a supposed male crab, he thought that he had a case of protandry until careful examination of the moult revealed the presence of the full number of abdominal appendages characteristic of the female. There is an exceedingly slight difference in the shape of the abdomen, which is a very little broader, and does not taper quite so much as in the male, while the sides of the segments are slightly convex. The locking apparatus is as well developed as in the male, and is very close to the oviducal apertures, which are on the sixth thoracic somite (Text Fig. 2). All four pairs of pleopods characteristic of the female are present, though not fully developed. The first two pairs (Plate V, Figs. 23, 24) are distinctly biramous, though there is not such a difference in length between the exopodite and endopodite of the first pair as there is in the adult. The third and fourth pairs are uniramous as in later stages. There are, at this stage, very few hairs on these appendages.

The ovary exists as paired narrow tracts of oocytes anteriorly; these join in the thorax, then divide again to extend into the abdomen. The ovary at this stage is not visible externally.

Similar male-like females have been recorded by Rathbun (7) as occurring in the American species, *P. maculatus*, *P. margarita*, *P. taylori*, and *P. concharum*. These hairy, male-like females are probably at first free swimming, but after a time enter a mussel where copulation takes place.

Females of this stage have been found with spermathecae full of sperm, others with spermathecae empty (Plate II, Fig. 4), while again some have been found with one spermatheca full and one empty (Text Fig. 3). In this stage the oviducts are narrow and their external apertures very small, so that the accurate adjustment of the tips of the long first copulatory appendages of the male during copulation must be a process of considerable difficulty, as evidenced by the occurrence of Stage I females in which insemination is not complete, one spermatheca being empty. One of the crabs found in this condition was a tiny one with a carapace measuring only 2.1 mm. across (Text Fig. 3). The difficulty of the process must be increased by the great discrepancy in size which often exists between individuals of a pair.

It would appear, therefore, that copulation takes place during this stage; that *P. pisum* is peculiar in copulating precociously at an extremely early age. The majority of the larger females examined have been found to have their spermathecae full of mature sperm, but occasionally an

adult occurs with the spermathecae almost if not quite empty. It is extremely probable that sperm from the first copulation is sufficient to fertilize several batches of eggs. The occurrence of an occasional adult female with empty spermathecae, would seem to point to the possibility that copulation may take place more than once. Males have been found all the year round within the same host as females of all stages, including those in berry, though it has been found that "a newly moulted female (adult) appears to have no charm for a male" (4).

There would appear to be no relation in age and size between the male and female of a pair; there is often a great difference, for young males

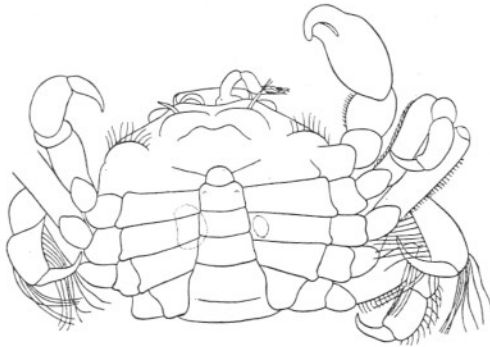


FIG. 3. Stage I female (carapace 2.1 mm. in width), with one spermatheca full and one empty. Stained with alum carmine and cleared in oil of winter green.

have been found with large adult females while the opposite may occur, though, of course, cases occur where there is little difference in size between individuals of a pair.

Orton (4) notes that: "It would appear that copulation normally takes place inside the host, and that the males visit mussels in their search for females, since unwary male crabs have been found with their legs or bodies trapped by the mussel closing its shell before the crab could get inside. These crabs survive the rough treatment by reason of their extraordinarily strong carapaces, and creep inside the mussel later when it must perforce relax and open its shell in order to breathe. The male-like female has a similarly hard carapace which prevents the animal being crushed to death if unluckily trapped by the mussel destined to become a host. Individual crabs have been found to be lacking a leg which might very well have been lost in this dangerous operation."

The change from the male-like female to the next stage is very striking. It undoubtedly depends upon and follows copulation, in this, offering a striking difference to Cancer (5), in which "ecdysis will not take place in

the female so long as there is a supply of spermatozoa in the spermatheca."

*Stage II* (Plate II, Figs. 5, 6). Females of this stage have been found with a carapace varying in width between 3.3 and 5.8 mm. The carapace is more or less circular; thin and membranous. It is translucent whitish or yellowish, without a colour pattern, although there are usually a few pale yellow spots on the ventral and dorsal surface. The front is advanced, and the eyes are as well developed, as in the male and male-like female.

In this and the following stages the chelipeds (Plate IV, Fig. 16) are slender, the palms being reduced in width, and there is only one row of setae on the lower edge of the chela. The walking-legs (Plate IV, Figs. 18, 20, 22) are more slender than those of the preceding stage, not so flattened and with very few hairs, though the degree of hairiness varies somewhat. The relative length of the legs is the same as in the male. The second and third legs bear only a scanty fringe of short hairs, attached near the upper margin on the posterior surface of the last three segments, which represents the much thicker and longer fringe present in the male.

The abdomen has increased in width, and is now more than half the width of the sternum. Anteriorly it extends beyond the chelae sterna, but is very little further forward than in Stage I. The locking apparatus has disappeared. The pleopods are further developed and more hairy (Plate V, Figs. 25, 26).

There is a certain amount of variation between individuals of the same stage, which may be due to differences in general conditions. Three specimens (one crab and two moults) have been taken with the abdomen rather narrower than that of the specimen figured, but with no other difference.

All specimens so far obtained, belonging to this stage, have been found to have the spermathecae densely packed with sperm.

*Stage III*. In this stage the abdomen has increased still further in width, and reaches further forward. The pleopods (Plate V, Fig. 27, 28) are rather more hairy than in the preceding stage.

Two variations of this stage occur:—

(a) The abdomen has increased greatly in width; at its middle it overlaps the sternum, but anteriorly extends very little if any further forward than in Stage II. Two crabs, with carapace 5.0 mm. and 4.75 mm. wide respectively, having these characters have been obtained moulted from crabs of the previous stage. The one with carapace 5.0 mm. across is figured in Plate II, Figs. 7, 8.

(b) The abdomen is only slightly wider than in Stage II, but reaches further forward. The two specimens which have these characteristics

are both 5.0 mm. wide. The field note on the specimen figured in Plate II, Figs. 9, 10, is "trace of gonad seen through carapace." The second one showed no sign of gonad externally. It is thought that these two crabs should be placed in Stage III, but they have not been verified by moults.

*Stage IV* (Plate III, Figs. 11, 12). Females of this stage have a carapace varying in width between 6.5 and 16 mm. The carapace is rather wider than long; smooth, shining, and rather stiffer than in the preceding stages. Some specimens have yellow spots on the ventral surface and legs, others are without them. The spots appear to consist of three or four cells in a stellate arrangement. There may also be scattered black and red chromatophores on the dorsal and ventral surfaces, but in none of the stages after Stage I is there any indication of a colour pattern such as Bell (1) both describes and figures for the adult female of *P. pisum*.

The front is less advanced than in Stage III, and though the eyes are very small they are still visible from the dorsal surface.

The abdomen in this stage reaches just posterior to the propodites of the outer maxillipeds, when the latter are covering the mouth. The abdomen is broad and overlaps on to the coxopodites of the legs. It is deeply hollowed, as is also the thorax, though to a less extent. The abdominal appendages are well developed and hairy (Plate V, Figs. 29, 30). The exopodite is rudimentary in the first pleopod, but very long and blade-like in the second. Hairs are present along the edge of the abdomen and sternum, and there is also a slight growth of hairs stretching in a semicircle across the thorax between the chelipeds, following the outline of the terminal segment of the abdomen. Scattered rosette glands occur on the pleopods and on the inner surface of the abdomen.

The degree of development of the ovary, of course, varies in different crabs. In specimens in which there are a considerable number of yolk-laden eggs, the ovary shows a deep red through the carapace, and where it has attained its full development it occupies the greater part of the body space, and almost the entire dorsal surface of the carapace appears of a deep red colour. The ovary extends nearly to the tip of the abdomen.

*Stage V* (Plate III, Figs. 13, 14). Females of this stage have been found between 9 mm. and 18 mm. wide. The carapace is wider than long, and often rather quadrilateral in shape. The front is very narrow, about one-fifth the width of the carapace, and is hardly visible from the dorsal surface. The eyes are feebly developed, being very minute and quite invisible from above.

The abdomen is rather larger than in the preceding stage. Laterally it overlaps on to the basipodites of the legs, while anteriorly it completely covers the mouth parts, reaching just posterior to the eyes. When the crab is feeding the last segment of the abdomen is bent rather sharply

inwards, so that the mouth is uncovered. The abdomen is deeply hollowed, as is also the thorax. Longer and more numerous hairs are found at this stage, on the edge of the abdomen and of the sternum, between the bases of the chelipeds and on the pleopods.

There is not a very great difference between Stage IV and Stage V; some crabs have been found with the abdomen reaching as far forward as in Stage IV, but as wide as in Stage V and vice versa. The variation in the degree of concavity of the abdomen may account for this difference, or it is possible that reproduction may take place in Stage IV, and that growth may go on after reproduction has commenced.

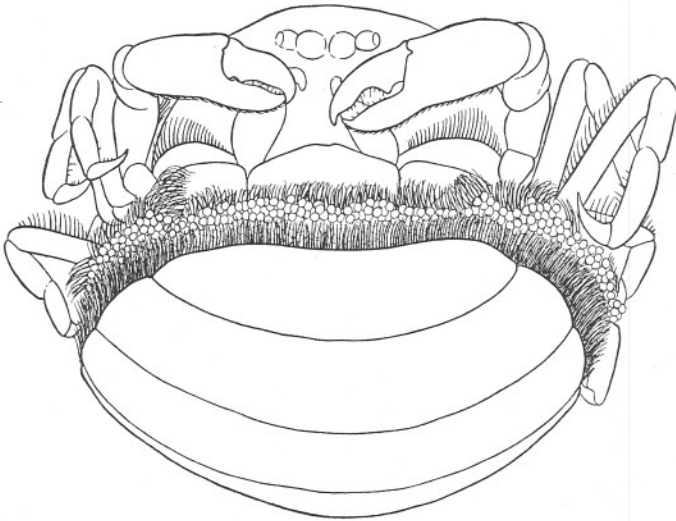


FIG. 4. Ovigerous female. Magnification, ca.  $4\frac{1}{2}$ .

*Ovigerous Female* (Text Fig. 4). The smallest berried female found had a carapace 7.5 mm. wide. The very numerous eggs are carried in the cavity formed by the hollowed thorax and deeply hollowed abdomen. The space between the side of the abdomen and the thorax besides being very small, is well guarded by long fringing hairs. The long blade-like exopodite of the second pair of pleopods, fringed with long and numerous hairs, fits along the inside of the gap as far forward as the fifth segment of the abdomen, and gives a double protection to the eggs.

In a good many instances the size of the pea-crab and its host was noted, and the figures are given in the accompanying table. It will be seen that there is a rough relationship in size between the female crab and its host, the larger crabs being found in the larger mussels. Hornell and Southwell (3) have noted this for *P. placunæ* found in the window-



pane oyster (*Placuna placenta*) from the coast of Okhamandal in Kattiarwar. They say : " Immature shells, as is natural, less frequently revealed the presence of commensal pea-crabs ; when they did occur the crabs were more or less immature. It would seem that the crabs grow towards maturity concurrently with their hosts."

Dr. Orton tells me that judging from the size of the mussels from which Pinnotheres have been taken, it is probable that the female crab attains sexual maturity easily in its first year. Additional evidence in favour of this is the scarcity of the early stages which would seem to point to the probability that the female passes through the various growth stages very rapidly. Of the first three stages, Stage I is perhaps the least scarce. It may be that a pause occurs here before a male enters the mussel and copulation takes place. During this time growth and moulting probably go on, but without a change of form, females of this stage having been found varying in size between 2.1 and 4.9 mm.

TABLE OF MEASUREMENTS OF FEMALE *Pinnotheres pisum* AND HOST (*Mytilus edulis*).

| Stage.             | Pea-crab<br>mm. in<br>width. | Mussel<br>mm. in<br>length. | Stage.   | Pea-crab<br>mm. in<br>width. | Mussel<br>mm. in<br>length. |
|--------------------|------------------------------|-----------------------------|----------|------------------------------|-----------------------------|
| Stage I (abnormal) | 4.0                          | 41                          | Berried  | 10.0                         | 58                          |
| I                  | 4.9                          | 62                          | "        | 10.0                         | 65                          |
| III                | 5.0                          | 60                          | "        | 10.0                         | 67                          |
| IV                 | 6.5                          | 80                          | "        | 10.0                         | 68                          |
| IV                 | 6.5                          | 82                          | "        | 10.0                         | 68                          |
| IV                 | 7.5                          | 56                          | "        | 10.0                         | 68                          |
| IV                 | 7.5                          | 58                          | "        | 10.0                         | 70                          |
| IV                 | 7.5                          | 68                          | Stage V  | 10.5                         | 68                          |
| Berried            | 7.5                          | 90                          | V        | 10.5                         | 73                          |
| "                  | 8.0                          | 53                          | IV       | 10.5                         | 84                          |
| "                  | 8.0                          | 58                          | Berried  | 11.0                         | 75                          |
| "                  | 8.5                          | 65                          | "        | 11.0                         | 76                          |
| "                  | 9.0                          | 60                          | Stage IV | 11.5                         | 79                          |
| "                  | 9.0                          | 65                          | V        | 12.0                         | 80                          |
| "                  | 9.0                          | 69                          | IV       | 12.0                         | 79                          |
| "                  | 9.5                          | 73                          | V        | 15.0                         | 104                         |
| Stage V            | 9.5                          | 72                          | V        | 15.0                         | 90                          |

The work recorded in this paper was undertaken at the suggestion of Dr. J. H. Orton, to whom I am indebted for advice, help, and information. I should like to express my thanks to him for sending me some of his

material as well as arranging for a further plentiful supply. The material came through the Marine Biological Association, Plymouth; a great deal of it from the Tollesbury and Mersea Native Oyster Fishery, Essex, through the kindness of Mr. French, and some from the Yealm Oyster Fisheries, Devon.

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#### EXPLANATION OF PLATES I TO V.

The outlines of the drawings were made with camera lucida.

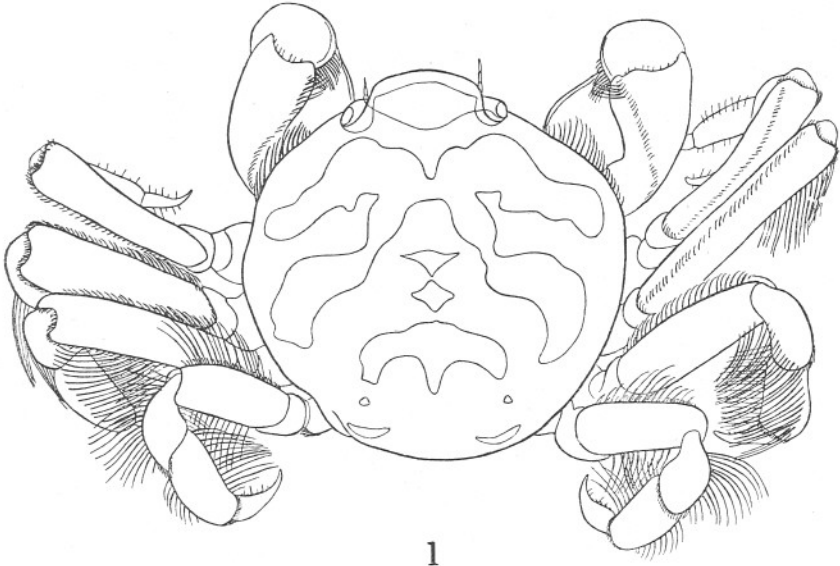
#### PLATE I.

*Pinnotheres pisum*, male  $\times$  ca. 8½.

FIG. 1. Dorsal view. The colour pattern is indicated.

FIG. 2. Ventral view.

PLATE I.



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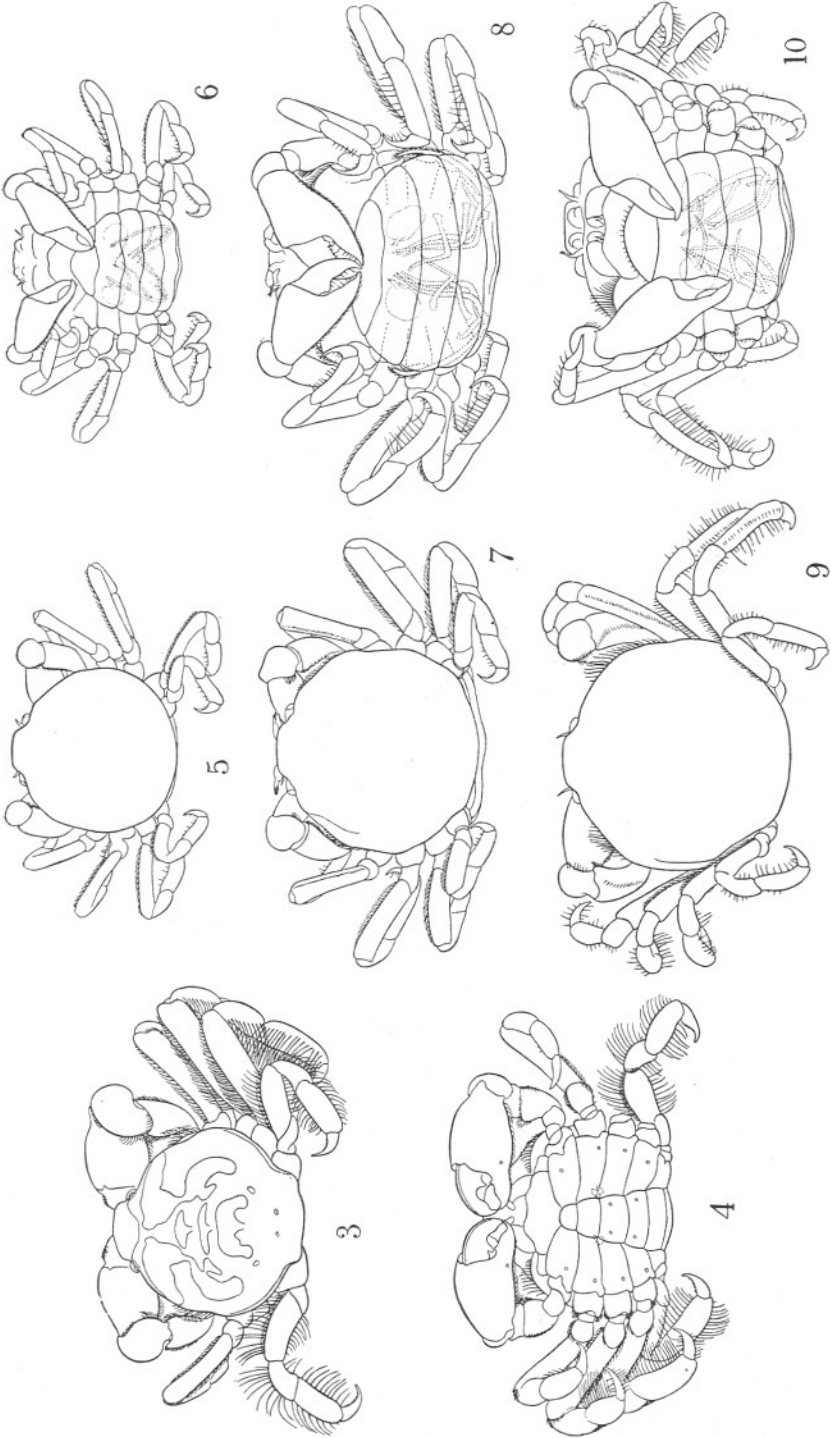
## PLATE II.

*Pinnotheres pisum*, female  $\times$  ca. 5.

The crabs figured in this plate and in Plate III were first drawn in outline, then soaked in acid alcohol, stained with alum carmine and cleared in oil of winter green.

- FIG. 3. Stage I, dorsal view. The colour pattern is indicated.  
FIG. 4. Stage I, ventral view. The empty spermathecae are shown by dotted lines.  
FIG. 5. Stage II, dorsal view.  
FIG. 6. Stage II, ventral view. The full spermathecae and the pleopods are shown by dotted lines.  
FIG. 7. Stage III (a), dorsal view.  
FIG. 8. Stage III (a), ventral view.  
FIG. 9. Stage III (b), dorsal view.  
FIG. 10. Stage III (b), ventral view.

PLATE II.



DEL. D. A.

## PLATE III.

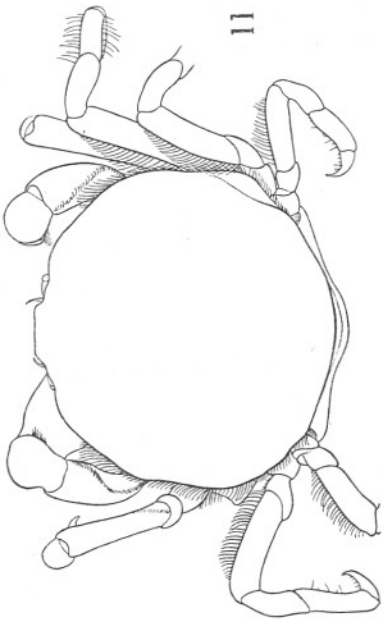
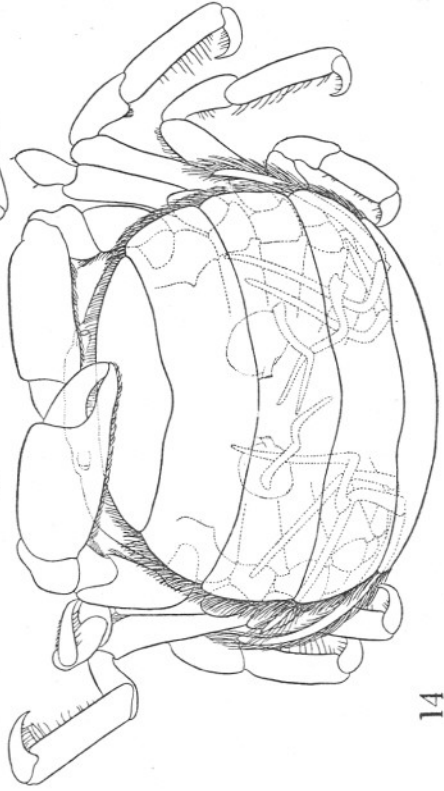
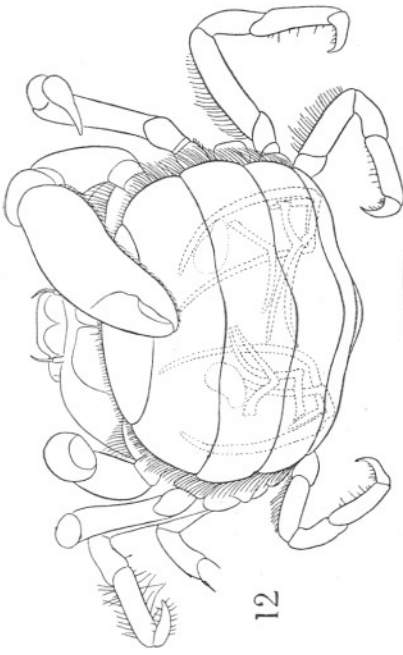
*Pinnotheres pisum*, female,  $\times$  ca. 5.

FIG. 11. Stage IV, dorsal view.

FIG. 12. Stage IV, ventral view. The spermathecae and the pleopods are shown by dotted lines.

FIG. 13. Stage V, dorsal view. The gonad is shown in outline. The abdomen is seen extending beyond the bases of the legs.

FIG. 14. Stage V, ventral view.



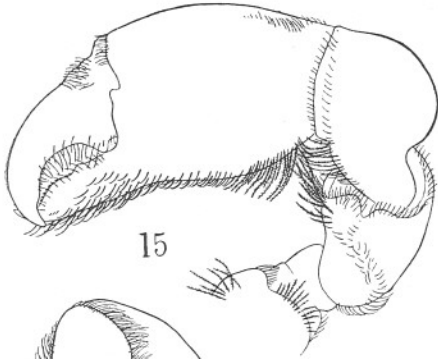
## PLATE IV.

Peræopods of right side of male and Stage II female, dorsal view,  $\times$  ca. 14.

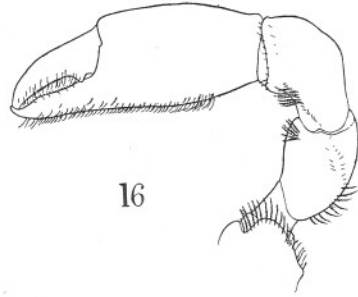
- FIG. 15. Cheliped of male.  
FIG. 16. Cheliped of Stage II female.  
FIG. 17. First walking leg of male.  
FIG. 18. First walking leg of Stage II female.  
FIG. 19. Third walking leg of male. The second walking leg is very similar, but slightly longer.  
FIG. 20. Second walking leg of Stage II female. The third walking leg is very similar, but slightly shorter.  
FIG. 21. Fourth walking leg of male.  
FIG. 22. Fourth walking-leg of Stage II female.



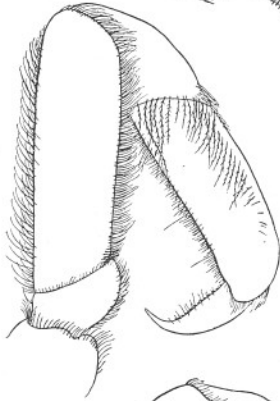
PLATE IV.



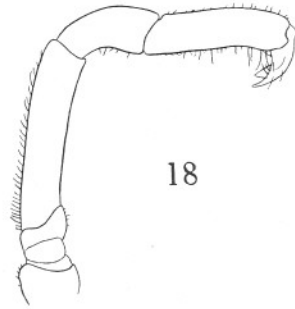
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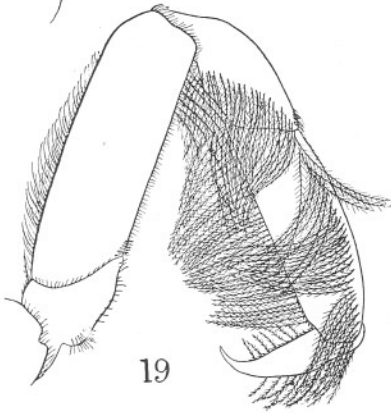
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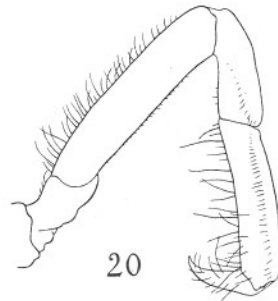
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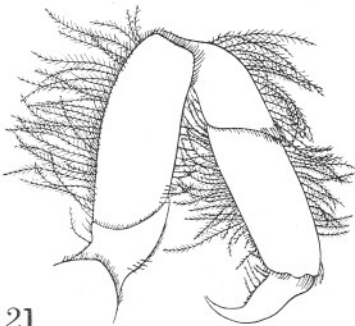
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DEL. D. A.



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## PLATE V.

First and second right pleopods of female.

- FIG. 23. Stage I female. First pleopod—drawn from a moult— $\times$  ca.  $57\frac{1}{4}$ .  
FIG. 24. Stage I female. Second pleopod ,, ,, ,,  $\times$  ca.  $57\frac{1}{4}$ .  
FIG. 25. Stage II female. First pleopod,  $\times$  ca.  $17\frac{1}{2}$ .  
FIG. 26. Stage II female. Second pleopod,  $\times$  ca.  $17\frac{1}{2}$ .  
FIG. 27. Stage III female. First pleopod,  $\times$  ca.  $17\frac{1}{2}$ .  
FIG. 28. Stage III female. Second pleopod,  $\times$  ca.  $17\frac{1}{2}$ .  
FIG. 29. Stage IV female. First pleopod,  $\times$  ca.  $12\frac{1}{2}$ .  
FIG. 30. Stage IV female. Second pleopod,  $\times$  ca.  $12\frac{1}{2}$ .

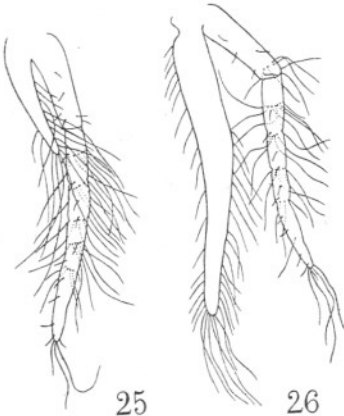
PLATE V.



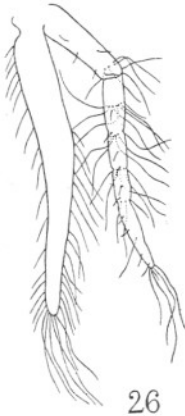
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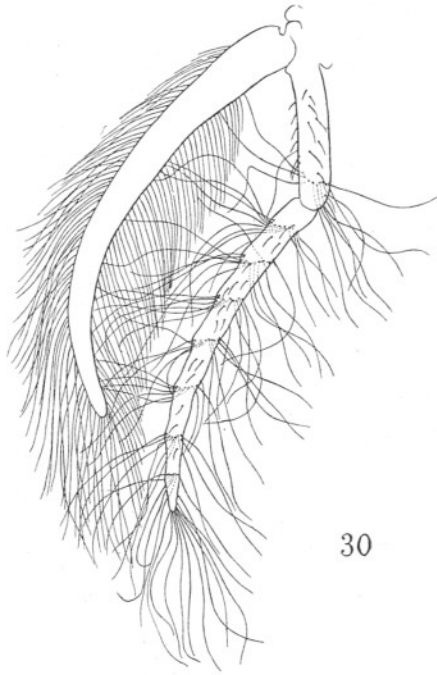
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