Studies of the Plymouth Brachyura. II. The Larval Stages of Ebalia and Pinnotheres.

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With 2 Plates and one Figure in the Text.

FURTHER study of the larval crabs of the Plymouth district has resulted in the elucidation of many more life-histories. Amongst these perhaps some of the most interesting are Ebalia and Pinnotheres. These genera, placed by systematists in widely different groups, resemble one another closely in many details in their larval stages and are here purposely described together in order that a comparison may be made.

The genus Ebalia is the only one of the sub-tribe Oxystomata (using Borradaile's classification, 1907) represented in Britain, belonging to the family Leucosiidæ, sub-family Leucosiinæ. Pinnotheres is placed in the sub-tribe Brachygnatha, super-family Brachyrhyncha, family Pinnotheridæ.

The main form of the zoea of Ebalia is well known, having no dorsal spine to the carapace which is large and round, the rostral and lateral spines usually rudimentary and the telson hardly forked at all, but having the form of a flat plate slightly drawn out at each side and bearing six setæ in the emarginate centre. *Pinnotheres pisum*, the commonest and best-known British pea-crab, has no dorsal spine on the carapace, but the rostral and laterals are well developed, the latter bending down in a characteristic way. Figures of this zoea have been given by some of the earliest naturalists. The telson is peculiar in being three-lobed, with three setæ each side between the central and lateral lobes. *Pinnotheres veterum*, however, has all the spines of the carapace well developed, the telson being like *P. pisum*. Both Ebalia and Pinnotheres zoeae have a pronounced tendency to curl up in a ball, and a very important feature in both is the minute and very rudimentary antenna which is entirely without a spinous process.

There are three species of Ebalia at Plymouth—*Ebalia tuberosa* (Pennant), *E. Cranchii* Leach, and *E. tumefacta* (Montagu). Of these the first is much the commonest, and is the only one in which the whole life-history has been successfully worked out. This is described here

completely for the first time. There are two species of Pinnotheres in the district, the "Common Pea-Crab," *Pinnotheres pisum* (Pennant), which occurs very frequently in mussels on the ground, also occasionally in cockles and ascidians, and the rare "Pinna Pea-Crab," *Pinnotheres veterum* Bosc. living in Pinna and other bivalves, the larva of which has hitherto only been known from a very incomplete description by Gourret (1882). The eggs of *P. pisum* have been hatched out in the aquarium, but it has not been possible to obtain adults of *P. veterum* during the last two years. Its larva occurs in the Plymouth plankton and has been reared as far as the megalopa. These larvæ are described here fully for the first time and are so different from those belonging to *P. pisum* that a revision of the adult characters may be necessary in order to determine whether *P. veterum* should not be placed in a separate genus. The investigations of Hyman (1924) on the larval forms of the Pinnotheridæ show, however, that these vary to a very large extent, especially with regard to the carapace and the telson.

Genus **Ebalia.**

Ebalia tuberosa (Pennant).

This crab is common in the usual dredging-grounds on sandy bottoms in the Sound. Berried females are to be found from January to June, but are commonest in the spring. The eggs are completely covered and hidden by the large abdomen which fits tightly under the carapace.

The larval forms of Ebalia so far described are not certainly identified. Cano (1892) gives a good figure of a late zoea (fourth and last) of an Ebalia, calling it Plagusia sp. and afterwards correcting this to Ebalia. He does not, however, identify the species. Williamson (1915) figures the first zoea of an Ebalia without giving the species. His description and figures closely resemble *Ebalia tuberosa* which is described here. He also mentions a third stage (number of setæ on the maxillipedes not ascertained) which he obtained from a second stage with six setæ. Miss Jorgensen (1925) describes larval Ebalia from North Sea plankton which she thinks probably belong to *E. Cranchii*, the commonest species on the Northumberland coast. It seems likely (as she herself suggests) that here are two species, *E. Cranchii* and *E. tuberosa*, for she figures four zoeae which apparently do not all belong to the same species. There appear to be six setæ on the maxillipedes in all the later stages. Possibly Fig. 8, which seems to be a fourth zoea, really has eight setæ instead of six. As her specimens were preserved there is no colour to guide us. She gives a drawing of a megalopa, probably *E. Cranchii*, which, although few details are shown, resembles that of *E. tuberosa*.

The eggs of *Ebalia tuberosa* are bright orange-red. These were hatched

out into pre-zoeae in a small aërated aquarium in the Plymouth Laboratory in April, 1927. Egg, 0·28 mm. across when first extruded, 0·3 mm. across when ready to hatch. The pre-zoea cast the embryonic skin almost immediately and the first zoea appeared. Unfortunately these did not live, but others were obtained from the plankton, the second and third zoeae with six setæ to the maxillipedes, the fourth with eight. This last changed into the megalopa, and from the megalopa came the young crab. Thus we have the complete life-history of *Ebalia tuberosa*, and almost certainly the other species are very similar in their larval forms. The presence of six setæ on the maxillipedes of both the second and third zoeae is apparently a unique feature, for all the other genera of crabs known have normally six in the second zoea and eight in the third, whilst the fourth has ten. Thus the fourth zoea with eight setæ is only found in Ebalia so far as we know at present.

Pre-zoea (Plate I, Figs. 1–4), 1·2 mm. in length,* zoeal colours showing through the embryonic cuticle, orange, yellow, brown and black. Antennule and antenna each with two long setose spines; telson quite distinctly forked with the usual seven spines each side, six long setose and one short non-setose, the latter covering the spine representing the tip of the fork. These long antennal spines are specially interesting as the antenna of the zoea is only a rudimentary stump. The telson is also interesting as indicating the ordinary brachyuran type of larval telson, the forking becoming obliterated in the zoea whose very characteristic and peculiar telson is probably an adaptation to its mode of life.

First zoea (Plate I, Figs. 5, 6), 1·3 mm. in length. Usually curled up in a ball, and, although at first coming up to the top of the aquarium, it very soon descends to near the bottom. Carapace large, rounded, without dorsal spine, rostral and lateral spines rudimentary. Eyes sessile, antennules with two æsthetes and two spines; antennæ small uniramous stumps; mandible large with reticulated surface; first and second maxillæ of ordinary form; first and second maxillipedes, as always in the first zoea, with four setæ on the exopodites, endopodites of five and three joints respectively. Remaining thoracic appendages very rudimentary, hidden under carapace. Abdomen of five joints plus telson, second and third joints with lateral knobs, first joint with six hairs dorsally, the others with two each. Telson a triangular plate drawn out at each side to a small tooth, hind margin slightly emarginate with six setæ in centre. Colour of zoea when first hatched pale brownish with front pale yellow, an orange spot at the top of carapace; as it grows the colour becomes more red and the under part of thorax a brilliant crimson. The zoea moves about quickly, curling up its body by bringing

* As in the previous paper (Lebour, 1927), the length is taken from the front of the head to the end of the telson.

the abdomen round tightly under the carapace. It is usually to be found near the bottom, and this is also the case in its natural surroundings. When Plankton samples are taken from surface, mid-water, and near the bottom, the Ebalia zoeae almost always occur, if present at all, in the samples from near the bottom but not in the others. Miss Jorgensen states that they rarely appear in the surface samples, and Russell (1927) also records them from the deeper layers only. Here it seems that we have a reason for the peculiar form ; the dorsal spine is not only superfluous but possibly actually in the way if the larva is not to live in the upper water layers. The forked telson with its long spines helps the ordinary crab larva to keep near the surface, but when this is not needed the telson tends to be flat and without long spines, and in this way it is

TEXT-FIG. 1.—Second zoea of *Ebalia tuberosa*, about 1·68 mm. long (Scale A).

wrapped round the body more easily to form a ball. The same reasoning may possibly apply to the antennæ, which have no long spinous process.

Second zoea (Text-Fig. 1), about 1·68 mm. in length. Colours like the first. Eyes stalked, antennules, antennæ and mouth parts hardly altered, first and second maxillipedes with six setæ. Rudimentary legs under carapace. Abdomen and telson much the same as the first, no pleopods. Occurs in the plankton with the first zoea.

Third zoea (Plate I, Fig. 7), about 1·92 mm. in length. Colours like the first and second, but more intense crimson, and a large black chromatophore mixed with orange and red on the top of the carapace. Lateral spines slightly larger, sticking out from sides of carapace as pointed knobs. Antennules tending to be jointed, swollen at base, antennæ and mouth parts hardly altered, first and second maxillipedes with six setæ. Rudiments of other thoracic appendages slightly larger. Abdomen and telson much the same, but pleopods have appeared as short buds on second to fifth segments. Miss Jorgensen describes five pairs of pleopods. This third zoea is to be found in the bottom layers in the same way as the first and second.

Fourth zoea (Plate I, Figs. 8–13), about 3 mm. in length, obtained by

the third zoea casting its skin. From the length of the pleopods and form and size of the rudimentary thoracic limbs it is clear that this is the last zoea. Colour the same as in the third zoea. Antennule, jointed, with small branch, antennæ little altered, palp on mandible, eight setæ on first and second maxillipedes. Thoracic legs slightly jointed, the first leg large with chela showing. Abdomen still with only five segments plus telson, and only four pairs of pleopods which are long. Knobs and hair on abdomen as before and telson hardly altered. The fourth zoea still keeps in the lower water layers, and changes into the megalopa. Thus there are four zoeal stages in *Ebalia tuberosa*.

Various foods were given to these zoeae. Even the first zoea was actually seen to eat early echinoderm larvæ and early Pomatoceros larvæ from artificial fertilisations, and their intestines often contained debris mixed with green cells and diatoms. Unfortunately they did not live. It was only the later stages, third and fourth zoea and megalopa, that lived any time and changed their skins. The megalopa was fed on small pieces of mussel.

Megalopa (Plate I, Fig. 14), obtained from fourth zoea, 3 mm. in length. Deep crimson with yellowish legs. Carapace nearly smooth without dorsal spine, almost straight in front, very slightly curved so that it protrudes in centre, but no rostrum. All legs functional, and maxillipedes now are mouth parts. Hind legs without feelers on last joint. Abdomen with six segments plus telson and five pairs of pleopods, the last pair with six setæ, the others with eleven. The hind legs without feelers resemble the Oxyrhyncha (Spider Crabs) and are unlike the Brachyrhyncha in this way, with the exception of Pinnotheres and probably its allies. The megalopa changed to the young crab (Plate I, Fig. 15), which was easily recognisable as Ebalia. This was no longer red but a pale yellowish colour. The second and third young stages from this were recognisable as *Ebalia tuberosa*, having the raised cross showing on the carapace. First young stage 1·9 mm. across carapace, second young stage 2·5 mm. across. Others grew to later stages but were not measured.

The following dates show the changes of skin from a megalopa obtained in the plankton 14/6/26 :—

First young stage 14/7/26.
Second ,, ,, 17/9/26.

These are probably much longer than is natural, as *Portunus puber* reared in comfortable conditions changed about once a week.

The life-history of *Ebalia tuberosa* is now complete, and we know that there are four zoeal stages and a megalopa before the first crab stage is reached, and that it is hatched as a pre-zoea.

Genus **Pinnotheres.**

The larval forms of the Pinnotheridæ may differ to a large extent, even the species of Pinnotheres itself varying as to the number of spines on the carapace and form of telson. The larvæ of the two British species are so unlike that it seems improbable that they should belong to the same genus. There are, however, certain important characters which they have in common, such as the rudimentary antennæ, form of telson and abdomen, which show that they must be closely related.

Pinnotheres pisum Leach.

The " Common Pea-Crab " occurs frequently in the Plymouth district inside the common mussel *Mytilus edulis* and is also occasionally found in *Modiola vulgaris* and in certain ascidians. The berried female occurs in the late spring and early summer, June being probably the best month, July slightly less so, and rare specimens may occur in August, after which the spawning is usually finished. A good figure of the berried crab is given by Miss Atkins (1927).

The eggs are an orange-red changing to a brownish colour when ready to hatch. The early eggs measure 0·27 mm., late eggs 0·3 mm. Berried females with eggs nearly ready to hatch taken from the mussels were put in plunger jars with some empty shells as shelter and the eggs hatched out as pre-zoeae, which almost immediately cast the embryonic skin and emerged as first zoeae. Unfortunately these did not live, and although similar specimens were obtained from the plankton no later stages were found. It is therefore impossible as yet to know the complete life-history. *Pinnotheres veterum* was found to have only two zoeal stages, but *P. pisum* probably has three or more, because the first zoea is much further backward in development compared with that of *P. veterum* and has no trace of pleopods. It is interesting that the first zoea of *P. pisum*, although at first rising to the surface, very soon went down to the bottom where it fed, the intestine being full of debris. There is no dorsal spine, and the zoea curls itself in a ball in a very similar way to Ebalia. The form in both seems to be adapted for life near the bottom.

Hyman (op. cit.) states that the only feature serving to distinguish the larvæ of the Pinnotheridæ is the minute size of the antenna, as the telson in some forms may be of the normal forked type and all the spines of the carapace may be present. As we have seen above, however, the antenna in Ebalia is also minute, but both British species of Pinnotheres are recognisable by the telson which has three lobes. This resembles *P. ostreum*, described by Hyman, which differs in having no spines at all on the carapace.

Pre-zoea (Plate II, Figs. 1, 2), 0·80 mm. long. Embryonic spines, antennules and antennæ so thin that it was impossible to secure them, and the first zoea appeared almost immediately. Taken from the egg nearly ready to hatch, the pre-zoea has a telson with two lateral teeth outside each of the lateral lobes.

First zoea (Plate II, Fig. 3-6), 0·96 mm. long. Minute and nearly always curled up in a ball. Colour greenish, made up of black, yellow, and orange chromatophores. No dorsal spine to carapace, but laterals and rostral well developed, all bending down. This is the stage given by Thompson (1835), the illustrations being copied by Bell (1853), therefore it is one of the earliest crab larvæ known. Eyes sessile, antennules short with two æsthetes and one spine, antenna minute, rudimentary stumps, mouth parts of the usual type. First and second maxillipides with four setæ on exopodites, endopodites of five and three joints respectively. Carapace large, rounded, no dorsal spine, laterals directed downwards and outwards, rostral curved downwards and slightly outwards. Abdomen of five segments plus telson, second and third segments with knobs, telson with three lobes, the central one rounded and slightly longer than the outer lobes which end in points. Outside outer lobes the margin is crenulated. Three spines each side between central and outer lobes. No trace of pleopods.

Pinnotheres veterum Bosc.

Berried crab not obtained. This is a much rarer species, occurring in Pinna and occasionally in other mollusks. Zoeae occur in the plankton during late summer and early autumn (August to October). These appear indiscriminately from the surface to the bottom layers. Pre-zoea not seen, but first and second zoeae were obtained, the second being the last, which when kept in the Laboratory changed to the megalopa. A first zoea changed to the second, but it was not found possible to bring the megalopa to the crab stage. The zoea has the telson very much like that of *P. pisum*, but is much larger and has all the spines of the carapace present and well developed.

First zoea (Plate II, Figs. 7–8), about 1·52 mm. long. Colour pale brownish red merging into pale yellow with dark brown chromatophores on dorsal spine, carapace, antennæ, mandibles, lateral spines and abdominal segments. Eyes black, sessile. Dorsal spine 0·96 mm. long, slightly curved backwards and then straight. Lateral spines 0·65 mm. long, sticking out behind the body, slightly curved downwards and directed downwards, outwards and backwards. Rostral spine 0·72 mm. long, slightly curved inwards and outwards. Antennule with three æsthetes and one spine. Antenna a rudimentary stump. Mouth parts of the usual type. First and second maxillipedes with four setæ on the

exopodites, endopodites with five and two joints respectively. Rudiments of other thoracic appendages hidden by carapace. Abdomen of five segments plus telson. Pleopods present as small knobs on segments two to five. Second and third segments with lateral knobs. Telson with central lobe shorter than laterals, the latter pointed with one short and thick tooth on its outer margin, but no crenulations as in *P. pisum*. The zoea has a decided tendency to curl up in a ball, but the spines probably enable it to keep in the upper water layers. They were always found singly and were never common. The telson is very like the figure given by Gourret for Pinnotheres sp. (1882), which he says is the same as *P. veterum*. Otherwise his very incomplete description tells us little. He obtained his specimen of *P. veterum* from *Pinna truncata*. In my previous paper (1927) it has been suggested that his figure of Pisa is probably *Pinnotheres veterum*. A comparison of this with the present illustrations will show how very likely this supposition is. That my specimens belong to a Pinnotheres is certain, and these are totally unlike any Spider Crab. In Gourret's figure of Pisa the rudimentary antennæ are shown, but the separate telson and antennæ which he depicts evidently really belong to Pisa and resemble Inachus and Macropodia. Being interpreted thus, Gourret's Fig. 3 (Plate II) should be *Pinnotheres veterum*, and Figs. 4 and 5 should be Pisa.

Second zoea (Plate II, Figs. 9–10), about 2 mm. long. Like the first in colouring and form. Eyes stalked. Six spines to maxillipedes. Antennules pointed and biramous. Antennæ as in the first zoea. Thoracic legs well developed but hidden under carapace; palp on mandible. Abdomen with still only five segments plus telson, knobs as before on second and third segments. Pleopods long, four pairs only. Telson unaltered. The second zoea changed into the megalopa, there are therefore only two zoeal stages in this species.

Megalopa (Plate II, Fig. 11), 1·68 mm. long. Greyish brown in colour. Carapace smooth without rostrum, the front slightly produced so as to form an undulating margin. Last pair of legs without feelers. Abdomen still with only five segments plus telson, and four pairs of pleopods. An interesting fact is that the megalopa swims very little and is so like a crab that one would almost describe it as the first crab stage if it were not that the setose pleopods are present and that the megalopa occasionally swims with them. More often it is seen with the abdomen tucked in under the body as in the crab. Now *Pinnixia Sayana* Stimpson has, according to Hyman (op. cit.), a zoea changing directly into a crab without any megalopa stage. This stage has also only four pairs of pleopods. The megalopa of *Pinnotheres veterum* seems to be intermediate between the ordinary megalopa and this form of young crab. Unfortunately it was not possible to rear these megalopæ any further, as they

would not cast their skins nor enter the mollusks provided for them. It is possible, however, that had they been given young Pinna this might have been effected. As it was they lived some time without changing and then died.

The life-history of *P. veterum* must differ considerably from that of *P. pisum* as it has only two zoeal stages and is hatched in a very well-developed state, whilst *P. pisum* is much more backward and must almost certainly have three or more zoeal stages. Two such different larval forms should surely be an indication of distinct genera.

Comparison of Pinnotheres and Ebalia.

It is interesting to compare the two types which in many ways are much alike, and yet the adults are placed so widely apart.

Perhaps the most important feature which these zoeae have in common is the rudimentary antenna which is merely a stump. This may be useful to a larva living near the bottom, but it is also present in those members of the Pinnotheridæ which have ordinary forked telson and all the spines of the carapace present.

In both Ebalia and the Pinnotheridæ there is a tendency to reduce the forks of the telson so that it becomes a more or less flat plate with the long spines shortened, and the abdomen usually curls in under the body so that a ball is formed. The habit of rolling into a ball seems obviously of advantage in keeping down below, but the curious form of the telson is probably derived from the ordinary forked type, and many of the Pinnotheridæ have this forked telson. We may perhaps look upon these peculiar variations in shape of telson as the most extreme deviations which are of advantage as an aid to curling up the body, those with ordinary telson being perhaps the more primitive.

Both Ebalia and the Pinnotheridæ have the abdominal segments less than the normal number in the later stages and a consequent reduction in the pleopods, and knobs are present on the second and third abdominal segment in all zoeal stages. It is difficult to see any meaning in the knobs, the number of which is, however, characteristic in certain groups, but a reduction in pleopods may possibly be because the zoea keeps to the lower layers of water. The megalopæ of both Ebalia and Pinnotheres are of the same type, having no rostrum, a comparatively smooth carapace without spines, and the last joint of the last legs being without feelers. These are the only megalopæ of all the British crabs known (and nearly all have now been observed by myself) which have no rostrum, and the absence of feelers on the last joint of the last leg is characteristic of the Oxyrhyncha, all the known megalopæ of the Brachyrhyncha with the exception of Pinnotheres having them. The megalopæ of Ebalia and

Pinnotheres are strikingly alike, the chief difference being that Ebalia has the normal number of abdominal segments (six plus telson) whilst Pinnotheres has only the five which were present in the zoea. Ebalia thus has added a segment in the megalopa whilst Pinnotheres still keeps to one less than the normal.

The resemblances in these larval crabs are interesting if at present not readily explainable, and the adult morphology might well be revised, for larval characters are of great importance and should be taken into account in any system of classification even if they are chiefly to be explained as special adaptations to environment.

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EXPLANATION OF PLATES.

As in the previous paper, the figures are drawn to three scales, the pre-zoea and zoea to Scale A ; the megalopa, young crab, and crab carapace to Scale B, half the Scale of A, and the appendages and various details to Scale C, three times the scale of A. All agree with those of the previous paper in scale.

PLATE I. *Ebalia tuberosa.*

FIG. 1. Pre-zoea, 1·2 mm. long (Scale A).
FIG. 2. Antennule of Pre-zoea (Scale C).
FIG. 3. Antenna of same (Scale C).
FIG. 4. Telson of same (Scale C).
FIG. 5. First zoea, 1·3 mm. long (Scale A).
FIG. 6. First zoea, back view (Scale A).
FIG. 7. Third zoea, 1·92 mm. long (Scale A).
FIG. 8. Fourth zoea, about 3 mm. long (Scale A).
FIG. 9. Fourth zoea, abdomen (Scale A).
FIG. 10. Fourth zoea, back view of a more slender specimen (Scale A).
FIG. 11. Fourth zoea antennule (Scale A).
FIG. 12. Fourth zoea antenna (Scale A).
FIG. 13. Fourth zoea, cast skin, front portion showing rostrum (Scale A).
FIG. 14. Megalopa, 3 mm. long (Scale B).
FIG. 15. First crab stage, 1·9 mm. across carapace (Scale B).
FIG. 16. Second crab stage, 2·5 mm. across carapace (Scale B).

PLATE I.

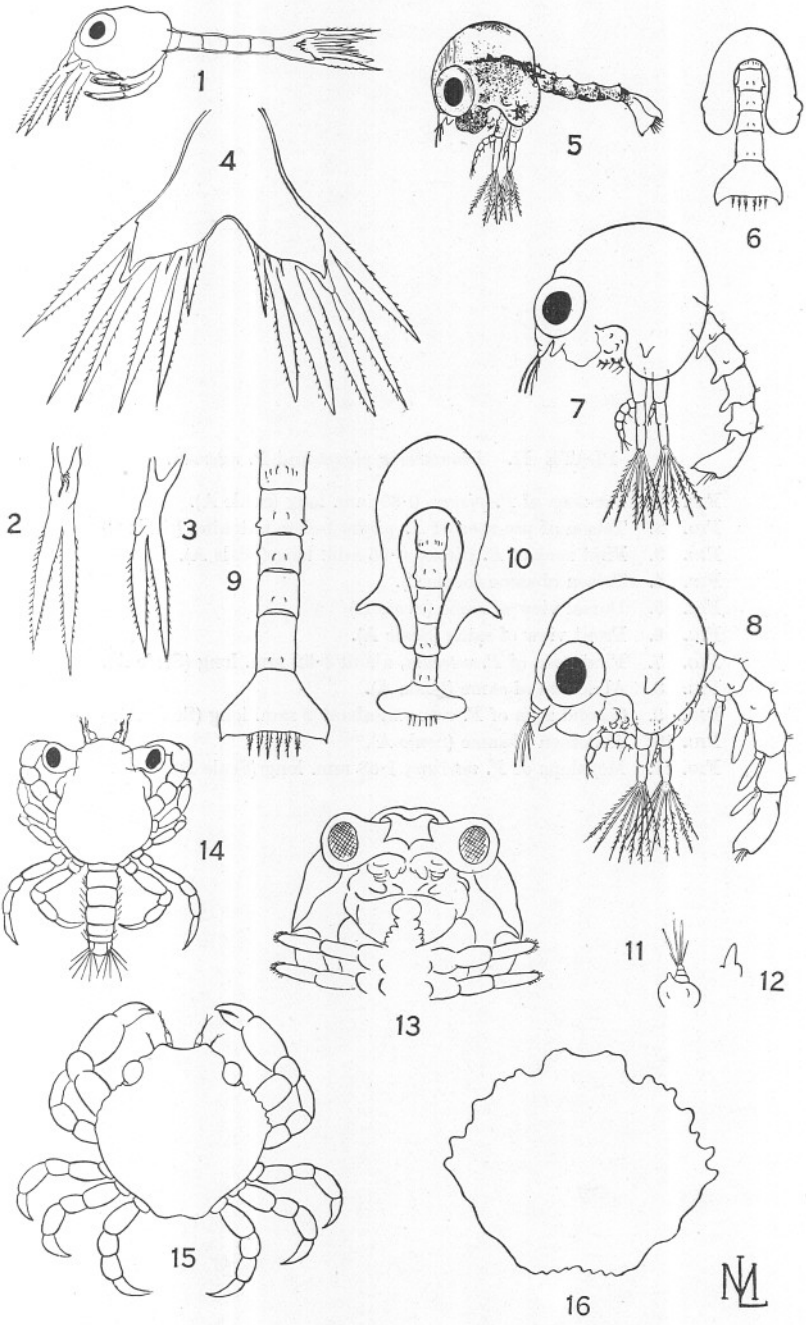
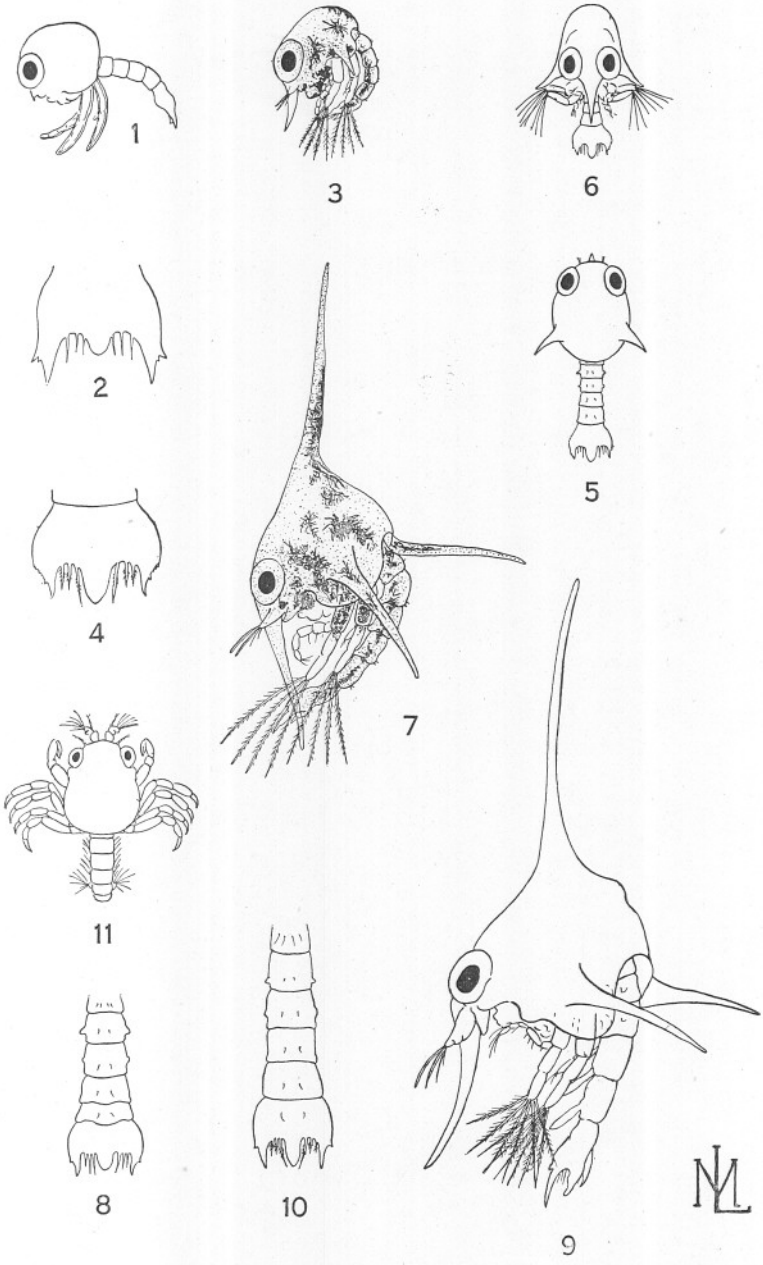


PLATE II. *Pinnotheres pisum* and *P. veterum*.

FIG. 1. Pre-zoea of *P. pisum*, 0·80 mm. long (Scale A).
FIG. 2. Telson of pre-zoea of *P. pisum* before hatching (Scale C)
FIG. 3. First zoea of *P. pisum*, 0·96 mm. long (Scale A).
FIG. 4. Telson of same (Scale C).
FIG. 5. Dorsal view of same (Scale A)
FIG. 6. Front view of same (Scale A).
FIG. 7. First zoea of *P. veterum*, about 1·52 mm. long (Scale A).
FIG. 8. Abdomen of same (Scale A).
FIG. 9. Second zoea of *P. veterum*, about 2 mm. long (Scale A).
FIG. 10. Abdomen of same (Scale A).
FIG. 11. Megalopa of *P. veterum*, 1·68 mm. long (Scale B).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