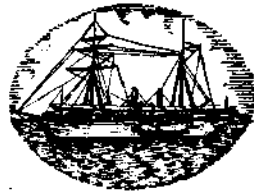


SYMPOSIUM ON CRUSTACEA

PART III



**MARINE BIOLOGICAL ASSOCIATION OF INDIA
MARINE FISHERIES P.O., MANDAPAM CAMP
INDIA**

PROCEEDINGS
OF THE
SYMPOSIUM ON CRUSTACEA

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PART III



SYMPOSIUM SERIES 2

MARINE BIOLOGICAL ASSOCIATION OF INDIA
MARINE FISHERIES P.O., MANDAPAM CAMP
INDIA

**ON AN INSTANCE OF PARASITISATION BY THE PEA-CRAB (*PINNOTHERES* SP.)
ON THE BACKWATER CLAM [*MERETRIX CASTA* (CHEMNITZ)] FROM INDIA,
WITH A REVIEW OF THE WORK ON THE SYSTEMATICS, ECOLOGY
BIOLOGY AND ETHOLOGY OF PEA CRABS OF THE GENUS
PINNOTHERES LATREILLE***

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ABSTRACT

A few species of the genus *Pinnotheres* Latreille are known to be definite parasites of some bivalves, while the great majority of the pea-crabs may be classed as obligate commensals and live in bivalve molluscs, echinoderms and ascidians.

The backwater clam *Meretrix casta* (Chemintz) from Malpe, on the west coast of India was found to be infested with a species of the pea-crab and a careful study of the infected clams indicated definite damages caused by the crab to the gills, mantle, gonad and digestive gland of the host indicating a clear case of parasitism. Descriptive account of the pea-crab, the meat weight-total weight ratio in the infected and uninfected clams, and other details are dealt with here.

This study has led us to draw up a brief review of the work so far carried out on the species of the genus *Pinnotheres* on aspects such as, growth stages; sex ratio and abundance; sexual dimorphism; ethology; ecology; physiology; effects of parasitism on host; parasites of pea-crabs of the genus *Pinnotheres*, etc. This coverage also includes a list of the known species of *Pinnotheres* from the Indo-Pacific, Atlantic and the contiguous seas with their known hosts and other details.

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INTRODUCTION

ON November, 25, 1960, one of us (E.G.S.) made a collection of backwater clams, *Meretrix casta* (Chemnitz), from a creek at Malpe on the west coast of India. A few of the clams opened at the time revealed the presence of one or more pea crabs within the mantle cavity, and the larger females were all found to be ovigerous. In order to see the incidence of infestation, as well as to identify the crab, about 450 clams were collected at the time. Unfortunately, it has not been possible to revisit Malpe subsequently to make any further observations on this association. In the course of examining the material in detail we have found damages in the soft tissues of the host which could have been caused only by the crabs they were harbouring, thereby justifying the categorising of the crabs as facultative parasites.

A perusal of the literature in this connection, as well as for identifying the crab, indicated the great need for a review of the available work on the systematics, biology, ecology, and behaviour of pea-crabs, especially of the genus *Pinnotheres* Latreille. Thus, in addition to our observations on the aforesaid instance of parasitic association, we have tried to cover here the general problem of commensalism and parasitism as pertaining to pea-crabs; a list of the known species of pea-crabs of the genus *Pinnotheres* with data on distributional range and host records wherever available; and an annotated bibliography of the works hitherto carried out on the species of *Pinnotheres*. An up-to-date list of species of *Pinnotheres* from the Indo-Pacific and Atlantic Oceans and contiguous Seas, it was felt, would be useful, as during the last 47 years since the publication of a review of the Indo-Pacific Pinnotheridae (excluding west coast of America) (Tesch, 1918) at least 21 new species have been described from various parts of the Indo-Pacific.

In a critical treatment of some of the species of the genus *Pinnotheres*, Gordon (1936) has laid stress on one important character, namely asymmetry in the appendages of pea-crabs, which has not been given due consideration by most of the earlier workers while describing and drawing up synopsis for the identification of the species. As to the biology of pea-crabs, recent studies on species such as *Pinnotheres ostreum* Say, *P. pisum* Pennant, *P. sinensis* Shen, etc., have added considerably to our knowledge about the habits and activities of these crabs as commensals and facultative parasites. Excellent studies on the physiology of commensalism of some marine invertebrates conducted during the last few years by Davenport and others have added to our understanding of the commensal behaviour of pea-crabs. The complete life-history stages is now known for at least one species, *P. ostreum*, while one or more stages have been described for a few of the other species from different parts of the world. In a way a review of this nature is also meant to draw attention to the large gaps that have yet to be filled in the study of pea-crabs. The scope of the work has necessitated the division of the subject-matter into four parts as dealt with below.

We wish to express our sincere thanks to Dr. S. Jones for his kind encouragement throughout the course of this work. Our thanks are also due to Mr. S. K. Banerji and Mr. S. K. Dharmaraja of this Institute for their help in the statistical part of this paper, and to Mr. N. K. Prasad for assisting in the preparations of the drawings. In the course of this work we have also received much needed literature from Dr. Aage M. Christensen, Marinbiologisk Laboratorium, Helsingor, Denmark; Dr. C. H. Edmundson, B. P. Bishop Museum, Honolulu, Hawaii; Dr. John S. Garth, Allan Hancock Foundation, University of Southern California, U.S.A.; Dr. J. J. McDermott, Department of Biology, Franklin and Marshall College, Lancaster, Pa., U.S.A.; and Dr. A. Daniel, Zoological Survey of India, Calcutta, to whom our thanks are due.

I. AN INSTANCE OF PARASITISATION OF THE BACKWATER CLAM *MERETRIX CASTA* (CHEMNITZ) BY *PINNOTHERES* SP.

MATERIAL AND METHODS

Material.—450 specimens of the clam *Meretrix casta* ranging from 18.4–30.5 mm. in length, from a creek mouth at Malpe, west coast of India, collected on 25-11-1960. Most of the clams

were infested with *Pinnotheres* sp. and the material was preserved in formalin diluted to 5% strength with water from the locality.

Methods.—The total wet weights of the clams were noted to the nearest milligram. When the preserved clams were opened, the location and number of pea-crabs on either side of the viscera were noted along with damages, if any, caused to the soft parts of the host. In instances where data were taken for study of the clam meat weight—total weight ratio, the actual weight of the crab or crabs in the individual clams were noted. The wet meat weight of the clam was taken after pressing it gently between blotting-paper to remove excess moisture. For this study clams whose shells were tightly closed were used. The crabs once removed from the host have been preserved in 70% alcohol.

A small subsample of unopened clams numbering 40 specimens has been deposited in the research collections of the Central Marine Fisheries Research Institute, Mandapam Camp.

DESCRIPTION OF *PINNOTHERES* SP.

An examination of 214 crabs showed that they are referable to a single species. The existing literature does not permit keying down the specimens to any of the known species, except indicate affinities to *P. parvulus* Stimpson in a few diagnostic characters such as the insertion of the dactylus of the external maxilliped to the inner margin of the propodus, the dactylus being styliform and not surpassing end of propodus; the dactyli of the fourth pair of walking legs being the longest; and the carapace being hardly 1·2 times as broad as long. Since it is generally felt that the genus *Pinnotheres* Latreille is badly in need of a revision on a world-wide basis, we do not want to add to the burden of a reviewer by designating a new species name for our material. The description given should help in its eventual placement in the system.

Descriptions and illustrations are given here of the ovigerous female which predominate in numbers; the hard-shelled (Stage I) and the soft-shelled (Stage II) stages of female; non-ovigerous female; and hard-shelled (Stage I) and soft shelled (stage II) stages of male.

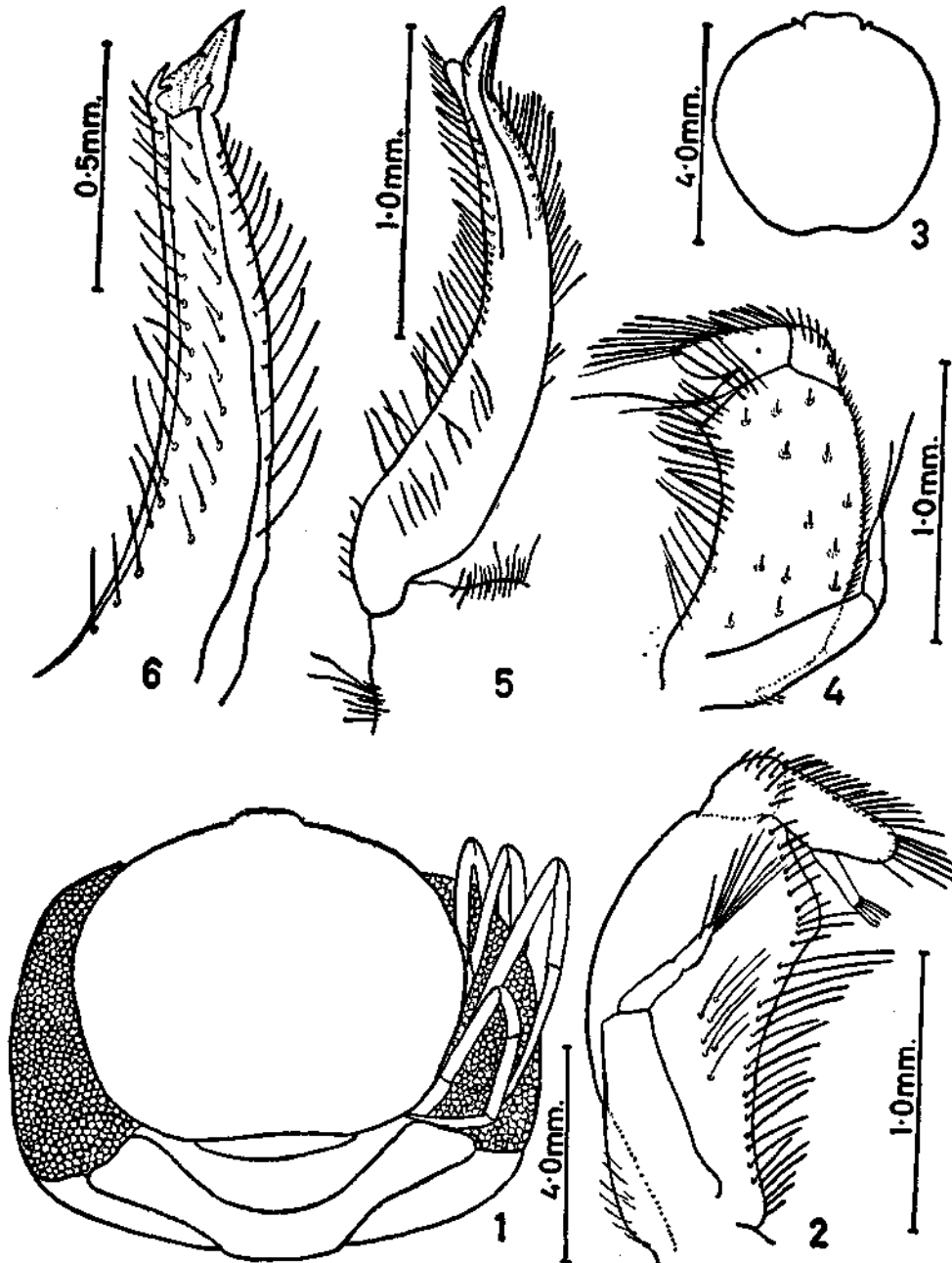
1. OVIGEROUS FEMALE

(*Text-Fig. 1: 1, 2; Pl. I, Figs. C-D*). The carapace is slightly broader than long (about 1·2 times) and consequently appears subquadrate to almost orbicular in outline, curving downwards towards the anterior and lateral margins. The surface of the carapace is smooth and naked. The front which is inconspicuous, hardly projects beyond the anterior margin of the carapace and has a straight anterior border. The minute ovate orbits are barely visible dorsally.

The merus-ischium of the external maxilliped is large, the outer (anterior) margin evenly curved and so also the inner border which abruptly tapers towards the distal end. Long hairs are implanted along the inner border from base to distal end and a few such hairs are also seen laterally about mid-length of the segment. The greatest width of the merus-ischium is about 2·3 times contained in its length. The carpus is conspicuously short, being hardly 1·5 times longer than broad. The propodus is relatively longer and more or less uniformly broad and bluntly rounded at the tip. Its breadth at the point of insertion of the dactylus is about 2·3 times contained in its length. The dactylus is long, slender and uniformly broad (not tapering) and reaches to a level with the tip of the propodus. The distal margin of the carpus, the outer margin and tip of the propodus and the tip of the dactylus bear short to moderately long setaceous hairs (*Text-Fig. 1: 2*).

The palm of the cheliped is slender, smooth laterally and elongate, being 3·25 times its greatest height and about 2·5 times as long as the finger. The latter is also narrow and slightly curved towards the tip. The fixed finger is also of almost the same size and shape as the movable finger and both have their inner margins fringed with hair. No conspicuous tooth is seen on the inner margin of the fingers except a fringe of minute serrations or undulations. Along the distal half

of the base of the palm and continued along the lower margin of the fixed finger to its tip is a row of short hairs.



TEXT-FIG. 1. *Pinnotheres* sp. (1) Dorsal view of ovigerous female. (2) external maxilliped of same. (3) Carapace of hard stage male. (4) External maxilliped of same. (5) Copulatory pleopod of same. (6) Distal half of copulatory pleopod of soft stage male (Stage II) of same.

The walking legs are slender, moderately elongate and subequal, the third pair being the longest. The second pair is longer than the first pair, but slightly shorter than the fourth pair. The propodus is longest in the third walking legs which on its inner side distally bears two or three long silky hairs. The dactyli of the walking legs show a progressive increase in size from the first leg to the fourth leg. Those of the first three legs end as slightly recurved claws. Barb-like short hairs are present along the inner margin of the dactyli of the first two walking legs and the dactyli of the third pair of walking legs have in addition a few long silky hairs. The dactyli of the fourth pair of legs are conspicuously elongate, being almost as long as the propodus, and having moderately elongate hairs along the inner margin.

No marked colour pattern is noticeable except the light brown broad transverse band across the palm of each cheliped.

2. FEMALE—STAGE I (HARD-SHELLED STAGE)

This is represented by a single specimen in the collection which happens to be also one of the smallest specimens examined having a carapace length of 3.0 mm. and width of 3.4 mm. Externally it shows a strong resemblance to the hard-shelled male (Stage I), but the differences are many. The chelipeds and walking legs appear relatively longer and are not hairy. The pleopods are digitiform and bifid, bearing long setae apically. This contrasts with the copulatory pleopods of the male at this stage which, when the abdomen is flapped open, stands erect prominently.

3. FEMALE—STAGE II (SOFT-SHELLED STAGE) (*Plate II, figs. C-D*)

One specimen with carapace length of 4.0 mm. and width of 4.2 mm.; abdomen broadly circular unlike in male; walking legs and chelipeds elongate and slender, not hairy. Externally the only noticeable difference seen between soft-shelled males (Stage II) and this stage females is in the shape of the abdomen.

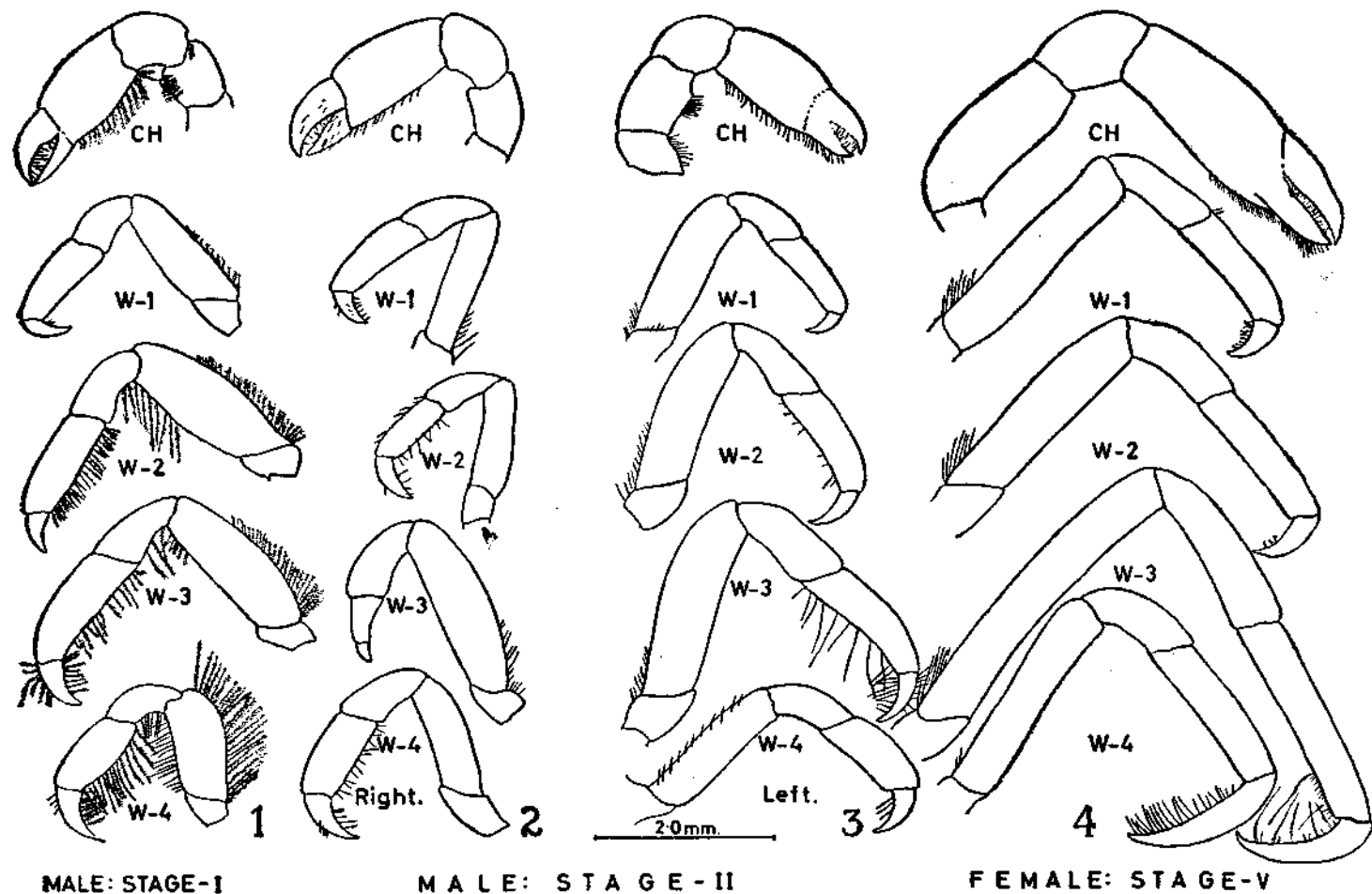
4. FEMALE—STAGES IV AND V (ADULT)

Six specimens of adult non-ovigerous females are present in the collection. Except for the non-attachment of the eggs there is hardly any difference between these specimens and the ovigerous females described above. The broad cupped 'petal-like' abdomen is very characteristic, and as wide as or slightly wider than the carapace. The differences between Stage IV and Stage V in the female are not great and it is likely that a few of the above-mentioned specimens may be border cases between the two stages. All ovigerous females represent Stage V.

5. MALE—STAGE I (HARD-SHELLED STAGE) (*Pl. I, Figs. A, B; Text-Figs. 1: 3-5*)

The carapace is orbicular, being very slightly broader than long, and with the margins curving downwards. The front projects out, is conspicuous and is slightly notched in the middle. The orbits and part of the antennae are seen when viewed from dorsally.

The merus-ischium of the outer maxilliped has the general shape as in the female. However, the dactylus of the propodus is short and slender and falls much short of the tip of the propodus. Unlike in the female, the dactylus is tipped with only two long silky hairs. In addition, the inner margin of the merus-ischium is implanted from base to distal margin with more numerous long setaceous hairs, and the outer margin is bordered with short stout hairs, similar hairs also being present along the outer border of the carpus. The hairs along the outer margin of the propodus are denser and those at the outer tip are relatively more elongate. Along the lateral sides of the merus-ischium are a number of short hairs.



TEXT-FIG. 2. *Pinnotheres* sp. Cheliped and walking legs in males and females: (1) Hard stage male (Stage I) (2 and 3) Soft stage male (Stage II) showing asymmetry of appendages on the left and right sides in the same individual. (4) Ovigerous female (Stage V).

As will be seen from Text-Fig. 2: 1, the chelipeds and the walking legs are relatively shorter, stouter, and bear more hairs, the disposition of which may be seen from the illustrations. The third pair of walking legs are the longest and the dactyli bear moderately elongate setae along the inner and outer margins. The dactyli of the first two legs are more or less equal in length and shorter than the third, which in turn is about three-fourths the length of the dactyli of the fourth leg. The hairy appendages are indicative of the free-swimming habit of the crab during this stage.

The male copulatory pleopod is shown in Text-Fig. 1: 5.

No conspicuous colour markings are seen except that the carapace which is hard is whitish.

6. MALE—STAGE II (SOFT-SHELLED STAGE) (*Pl. II, Figs. A-B; Text-Fig. 1: 6; and 2: 2-3*)

A few males in which the carapace is soft as in the female were also encountered in the collection. The appendages of these specimens are also less hairy as in the females, suggesting that they represent a stage beyond the hard-shelled stage. The carapace is more or less subquadrate, and again as in the female, the chelipeds and the walking legs are slender and relatively elongate.

The distal half of the copulatory pleopod of a specimen measuring 4.0 and 4.3 mm. in carapace length and width respectively is shown in Text-Fig. 1: 6. There appears to be no noticeable difference in the structure of the copulatory pleopod of this stage and that of the hard-shelled stage.

In the same specimen, marked asymmetry in the size of the chelipeds and walking legs of either side of the body was seen and this is indicated in the scale drawings of the appendages in Text-Fig. 2: 2-3. Asymmetry to this extent was not noticeable in the other specimens, although in a few ovigerous females, the length of the legs in a pair were not exactly equal.

The soft shelled males were also examined for external and internal parasites to find out if any such infestation of the hard-shelled male could result in a soft-shelled male resembling the female. However, there were no indications of any parasites. Differences between these two stages in the shape of the carapace, the relatively slender and longer chelipeds and walking legs which are devoid of much of the hair seen in the hard-shelled stage, rule out the possibility that such soft-shelled condition could be the result of decalcification in the original preservative (5% formalin).

FECUNDITY

The eggs in the ovigerous females were found to vary slightly in diameter. In the preservative the eggs are 'light brown' to almost 'greyish' and it is felt that this may depend on the duration of the attachment of the eggs, the 'greyish' eggs being attached over a longer period and consequently showing more embryonic development. The sizes were also found to vary accordingly, the diameter of the 'light brown' eggs being slightly lesser than that of the 'greyish' eggs. In the following table (Table I) the egg counts for six ovigerous females are given along with other details. While teasing out the attached eggs, as a few are liable to be damaged, the counts when ending in less than a hundred have been rounded off to the next hundred; e.g., 2468 has been rounded off as 2500, or 2736 to 2800. The actual counts excluding a few damaged eggs showed a range of 1688-2786 eggs (rounded off here as 1700 and 2800 respectively) in the six specimens examined.

TABLE I

	Length of carapace (mm.)	Width of carapace (mm.)	Total No. of eggs	Diameter of eggs (range in mm.)	Egg colour
	6.2	7.0	2,500	0.32-0.34	Light brown
	6.0	6.2	1,700	0.35-0.37	Greyish
	6.4	7.0	2,800	0.36-0.37	do.
	5.4	6.2	1,900	0.32-0.35	Light brown
	5.9	6.4	2,000	0.36-0.37	Greyish
	6.5	6.9	2,600	0.36-0.38	do.
Average	6.06	6.6	2,250

FREQUENCY OF OCCURRENCE OF *PINNOTHERES* sp. in *MERETRIX CASTA*

A total number of 379 clams out of the 450 were examined and it was found that 183 clams (48.3%) were infested with one or more pea-crabs. A further analysis of the frequency of occurrence of the pea-crabs in the infested clams showed the following position:

	No.	%
Number of infested clams out of 379 examined ..	183	..
Number of clams with single crab each ..	152	83.1
Number of clams with two crabs each ..	24	13.1
Number of clams with three crabs each ..	7	3.8

For sex-wise occurrence of crabs, stage of development, size, etc., 117 infested clams were specially examined. They had a total number of 136 crabs in the following stages of development and frequency of occurrence.

There were 82 females and 54 males as follows:

Female

	No.
Stage I (Hard-shelled stage) ..	1
Stage II (Soft-shelled stage) ..	1
Stage IV (Adult, non-ovigerous) ..	6
Stage V (Adult, ovigerous) ..	74
Total ..	82

Male

Stage I (Hard-shelled stage) ..	45
Stage II (Soft-shelled stage) ..	9
Total ..	54

The frequency of the single and multiple infestations is shown in the following table (Table II).

TABLE II

Infestation	No. of clams	Pea-crabs		Total No. of pea-crabs
		Female	Male	
1. Single infestation ..	101	65	36	101
2. Double infestation ..	13	13	13	26
3. Triple infestation ..	3	3	6	9
Total ..	117	81	55	136

A further analysis of the single and multiple infestations by the pea-crabs in the 117 infested clams examined shows the following:

	<i>Numbers</i>
<i>Single infestation—</i>	
Total number 101
Female—Stage I (Hard-shelled stage) 1
Female—Stage II (Soft-shelled stage) 1
Female—Stages IV-V (Adults) 64 (5+59)
Male—Stage I (Hard-shelled stage) 26
Male—Stage II (Soft-shelled stage) 9
<i>Multiple infestation—</i>	
A. Double infestation:	
Total number 13
Female—Stages IV-V (Adults) 13 (1+12)
Male—Stage I (Hard-shelled stage) 13
B. Triple infestation:	
Total number 3
Females—Stage V 3
Males—Stage I (Hard-shelled stage) 6

In all cases of double infestation, a male and a female were present in each clam, and in the three instances of triple infestation, the ratio was one ovigerous female to two males (Stage I). In the three instances of triple infestation it was also seen that one of the males is much smaller than the other, the carapace measurements (mm.) being:

No.	Female		Male		Male	
	L.	W.	L.	W.	L.	W.
1.	6.2	6.7	4.4	4.8	3.5	4.7
2.	6.2	6.7	4.5	4.9	3.7	4.0
3.	6.4	7.0	4.3	4.4	3.8	4.0

The very low percentage of triple infestations combined with the differences in the sizes between the males lead us to believe that one of the males had entered the clam inadvertently while seeking an uninfested clam or one infested only with a female.

The number of double infestations are also relatively low and here again it is possible that the males had entered inadvertently. This is possible as the females are all ovigerous and there is a much larger percentage of males showing single infestation. These appear to be plausible explanations for this manner of infestation seen.

As a matter of interest the location and disposition of the crabs inside the clam, namely whether they were found on the left or right side, positioned close to the gills or palps, etc., were noted. It is likely that some of the crabs could have moved to other positions at the time of preservation. However, the position was as follows: In the case of infestations with single crabs, out of 144 instances checked, 56 were found on the left side and 88 on the right side of the clam. In cases of multiple infestation, in some of the clams all the crabs were found on one side, either the right or the left with a few exceptions when they were seen on both sides. In all cases the crabs were seen inside the mantle cavity and the area of the gills was found to be by far the most haunted place, while a few were found in the anterior region of the foot, or near the labial palps.

EFFECT OF INFESTATION OF *Pinnotheres* SP. ON ITS HOST *Meretrix casta*

At the time of the removal of the crabs from the clam it was found that certain types of damages were present in the soft parts of the clams which are not likely to have been caused by any manner other than by the pea-crabs. A perusal of the literature showed that similar damages to soft parts of (bivalves) are known to be caused by some species of *Pinnotheres* (Strauber, 1945; Orton, 1921, 1931; McDermott, 1962; Berner, 1952; Sandoz and Hopkins, 1947, and others). A few of the non-infested clams we examined were also seen to show slight traces of damages and we presume that this may have been on account of earlier infestation of the clam by the hard-shelled stages of the crab which could have left the host, or could have been ejected by the latter.

Some workers have mentioned that the availability of food plays a role in the sexuality of oysters (Amemiya, 1929, 1935; Egami, 1935; Coe, 1934, and others). Heavy infestation of oysters resulting in hermaphroditic condition of the former has been reported by Awati and Rai (1931). In the present instance, as the clams were preserved, it was difficult to make any observations on the sexuality of the clams in relation to the infestation by *Pinnotheres* sp. In order to find out whether there was really any significant difference in the meat weight of infested and non-infested clams, 50 clams each of both categories were selected at random and the soft parts weighted to the nearest milligram. The weights graphically plotted (Text-Fig. 3) showed a wider spread and considerable overlap. An analysis of variance based on the meat weight of both categories indicated that the differences were not statistically significant. Since the data graphed showed wider spread, the weights were converted into logarithms but the result of the analysis given in (Table III) also shows the same results.

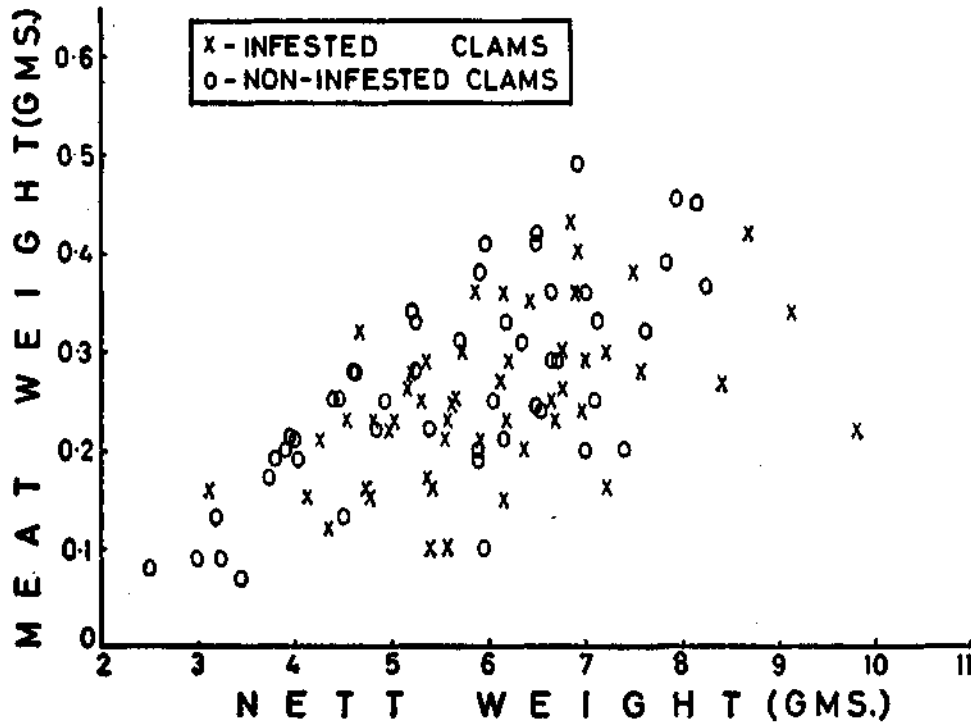
TABLE III

Analysis of covariance of linear regression of meat weight against shell weight to test the significance of differences among infested and non-infested Meretrix casta

Samples	D.F.	x^2	xy	y^2	b	D.F.	S.S.
Infested clams	49	0.4288	0.3604	1.4210	0.8405	48	1.1181
Non-infested clams	49	0.8245	0.9112	1.9567	1.1052	48	0.9587
Total	98	1.2533	1.2716	3.3867	1.0146	96	2.0768

Test of heterogeneity of regressions within the samples

Source of variation	D.F.	s.s.	M.S.	F
Deviation from individual regressions within samples	96	2.0768	0.0216	1.0964
Difference among samples	1	0.0197	0.0197	..
Deviations from average total regressions	97	2.0965



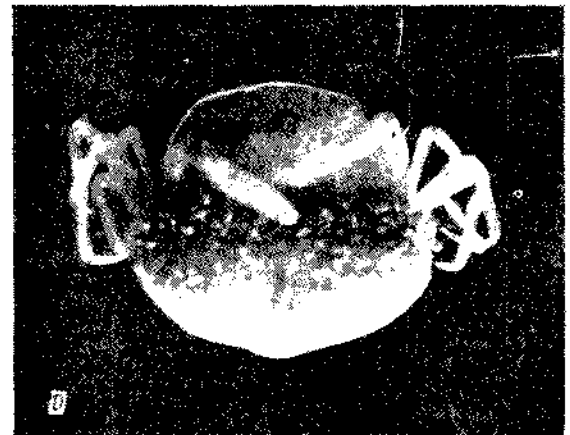
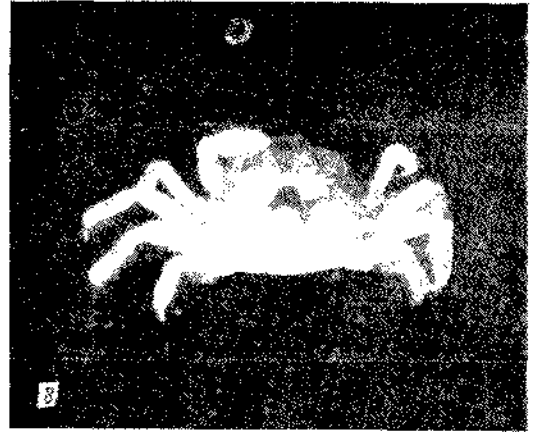
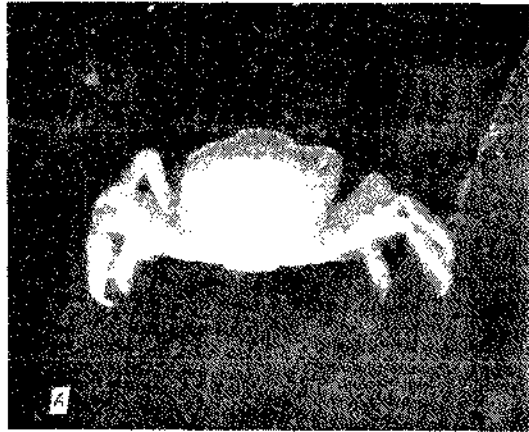
TEXT-FIG. 3. *Pinnotheres* sp. and *Meretrix casta*. Graph showing the meat weight-net weight relationship in two samples of *M. casta*, one infested and the other non-infested with *Pinnotheres* sp.

We are unable to give the reasons for this except presume that: (1) the damages noticed in the form of gill erosion, etc., to be presently discussed do not reflect in the weight to show any significant difference, or (2) the likelihood of clams once infested (earlier infested) being inadvertently included in the non-infested sample, or (3) the inclusion of infested clams which did not show any visual damage, in the sample studied. The above points arise as the selection of the clams for this study was made at random from infested and non-infested clams.

Injury to soft parts of the host:

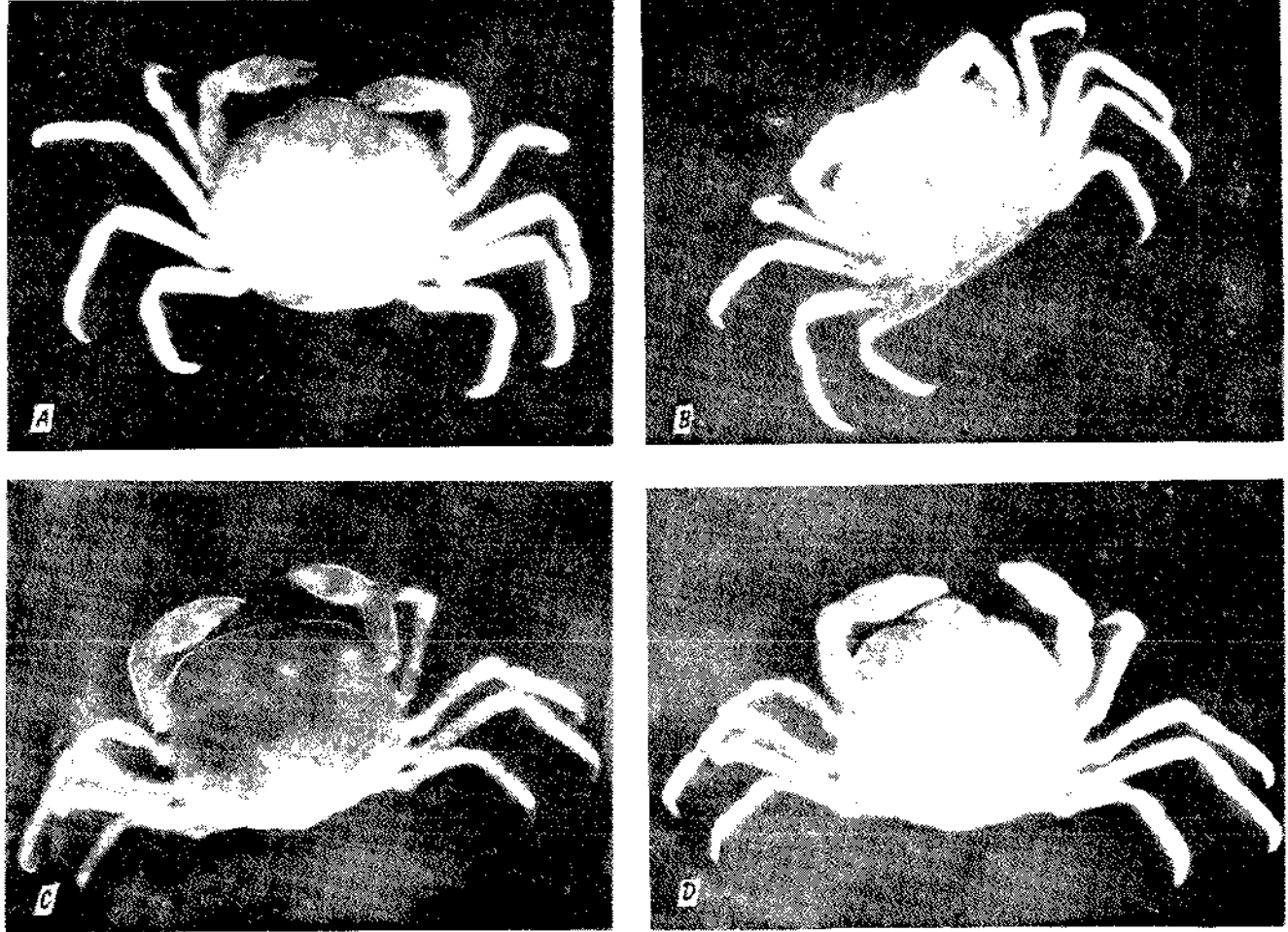
The damages caused by the crab on the soft parts of the clam were noticeable in various organs such as the gills, the gonad, the digestive gland and the mantle. The nature and extent of the damages noticed are discussed below.

1. *Gills* (Plate III, Figs. A-D).—The gills appear to be the organ most affected by the crab and various types of gill erosion and malformation were noticed. The lower margin of the gill,

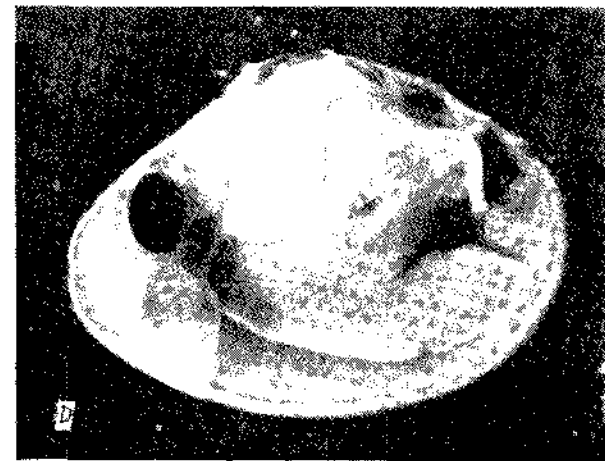
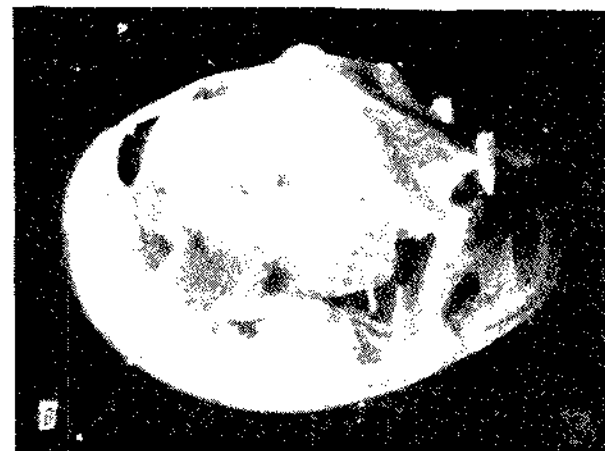


Pinnotheres sp.

(A) Dorsal view of hard-stage male (Stage I). (B) Ventral view of same. (C) Dorsal view of ovigerous female (Stage V). (D) Ventral view of same.



Pinnotheres sp.
(A) Dorsal view of soft-shelled male (Stage II). (B) Ventral view of the same. (C) Dorsal view of soft-shelled female (Stage II). (D) Ventral view of the same.



A-D. Four different types of gill erosion in *Meretrix casta* (Chemnitz) caused by *Pinnotheres* sp. (see Text)

laminae in many of the specimens were distorted and unevenly curled. In most cases the affected portion of the gill laminae is distinctly shorter than the unaffected portion and the functional part of the gills is restricted leaving a distal papery or membranous laminar portion (Pl. III, Fig. C). Whether the latter portion represents an area of regeneration or not is difficult to say. In some instances the erosion of the gills as a result of nipping or pinching of the margins by the crab is clearly noticeable (Pl. III, Figs. A-B). In a few cases the crab was found between the viscera and the gills with the carapace resting against the gonad of the clam. Whether this is its natural position or brought about during its struggle at the time of preservation is not understood. In some clams the margins of the gill laminae are wavy and often thickened in places suggesting malformation or healing. In an interesting case the distal half of the gill lamina was found to have been pinched off throughout its length with no apparent regeneration in evidence. In an extreme case it was found that the anterior halves of the gill laminae are completely damaged leaving a thin papery structure which is lying flapped on the functional posterior part of the lamina. A large lesion in the visceral mass is also noticeable (Pl. III, Fig. D).

2. *Digestive gland and gonads.*—In some of the infested clams, the digestive gland as well as the gonad are flacid with the outer skin loose. Often due to the lodging of the crab lateral to the gonad or the digestive gland, conspicuous depressions are seen, no doubt brought about by the pressure exerted by the crabs. How far this would affect the normal functioning of the gonads is not known.

GENERAL REMARKS

To our knowledge there is hardly any reference to Indian species of *Pinnotheres* the activities of which have been definitely reported to be parasitic in nature. Awati and Rai's (1931) remarks on *Pinnotheres* sp. affecting the sexuality in *Ostrea cucullata* is suggestive. Hence the present observations showing *Pinnotheres* sp. infesting *Meretrix casta* at Malpe more as a parasite than as a commensal should be of interest. Unfortunately, as already mentioned, neither subsequent collections to the one conducted, nor observations on live clams and the pea-crabs were possible. It is now known through the works of Strauber (1945), Christensen and McDermott (1958), and others that pea-crabs, the activities of which are definitely known to be parasitic could at times lead a commensal existence. This may depend to a great degree on fluctuations in the numbers of the pea-crab population in the oyster and mussel beds, the tendency towards parasitism being more pronounced with an increase in the crab population. It is likely that the single and multiple infestations of *Meretrix casta* by *Pinnotheres* sp. that we have noticed may be due to such a phenomenon, namely an abundance of the crabs in the area during November 1960. Such fluctuations in the occurrence or the non-occurrence of pea-crabs where bivalves occur are possible. Abraham (1954) reporting on the biology of *Meretrix casta* from Madras, does not mention anything about the occurrence of pea-crabs in the clams in that area. Dr. V. S. Durve of the Central Marine Fisheries Research Institute who is working on *M. casta* and with whom we had occasion to discuss this aspect informs us that he has not come across pea-crabs in the large samples of clams he has examined from Athankarai and the C.M.F.R.I. fish farm (Palk Bay).

In the case of *Pinnotheres ostreum*, parasitic on the American oyster *Crassostrea virginica* it has been reported that a good amount of damage is also caused by the multiple infestation of the host by the hard-shelled stages of the crab. The young pea-crabs are more likely to nip the gills and other tissues of the host. In addition, the hard unyielding carapace, due to friction may cause lesions in the soft parts of the host. In this connection also our observations seem to be of interest as we found gill erosion more commonly in the clams harbouring the hard-shelled stage of the male (Stage I) as well as this stage of the male when present with the ovigerous female.

In the course of carrying out this work we found that there was a great need to synthesise the available informations on the biology, ecology, and ethology of pea-crabs of the genus *Pinnotheres*,

especially to draw attention on the investigations successfully carried out in these fields in different parts of the world and at the same time highlight the several gaps that need filling. These are dealt with in the ensuing part.

II. REVIEW OF THE WORK ON THE ECOLOGY, BIOLOGY AND ETHOLOGY OF THE PEA-CRABS OF THE GENUS *PINNOTHERES*

The early Greeks as exemplified from the writings of Aristotle seem to have been aware of the association between pea-crabs and bivalves which they regarded as an example of friendship. General accounts of pea-crab associations are dealt with by various writers (Calman, 1909; Freame, 1943; Thompson, 1835; MacGinite and MacGinite, 1949; Mansueti, 1955; Ricketts and Calvin, 1952; Haven, 1957; Young, 1960, and others). Bashford Dean (1892) appears to be one of the first to observe that the activities of the pea-crab *P. ostreum* in its host were parasitic in nature, as the crabs affected the palps of the oyster which show thickened outgrowths, or are malformed or stunted. However, the great majority of pea-crabs, especially those of the genus *Pinnotheres*, are known to occur as commensals in bivalves, ascidians, holothurians, tubes of polychaetes, and even in brachiopods. Proven cases of *Pinnotheres* being a facultative parasite of bivalves are few, the notable instances being *P. ostreum* in the American oyster *Crassostrea virginica*; *P. pisum* in the mussel *Mytilus edulis* and *P. sinensis* in the Japanese oyster *Ostrea gigas*. We have herein reported an additional instance of *Pinnotheres* sp. in the backwater clam *Meretrix casta*.

LIFE-HISTORY

1. EGG DEPOSITION AND HATCHING

Information on ovigerous females is available for a few species. However, very little is known about the duration between egg deposition and hatching, nor is any information available about the duration individual females carry their eggs under natural conditions, but laboratory observations are available for some species.

Hart (1935) found that the eggs of an ovigerous *P. taylori* brought to the laboratory on 16 March 1933 did not hatch until the first week of May the same year.

Atkins (1955) has observed egg deposition and hatching in six specimens of *P. pisum* and found the egg bearing period to vary between 35 and 59 days. She attributed temperature differences to be an important factor responsible for the considerable delay in the duration between deposition and hatching noticed. In the case of a *P. pinnotheres* brought to the laboratory with eggs in the early stage, hatching took place after 40 days.

The seasons and stages during which egg deposition takes place in *P. ostreum* is given by Christensen and McDermott (1958). They also found that the egg carrying duration (in nature 3-5 weeks) to be much shorter in the laboratory. This is in agreement with the observations of Sandoz and Hopkins (1947) who obtained zoea from a *P. ostreum* carrying a light orange egg mass after 12 days in the laboratory.

2. DEVELOPMENT OF SPECIES OF *Pinnotheres* (LIFE-HISTORY STAGES)

Out of well over a hundred species of *Pinnotheres* described in literature, the complete or almost complete developmental stages are known for only two species, namely *P. ostreum* and *P. pisum*. Stray accounts of descriptions of one or more developmental stages are available for a few species and by far nothing is known about the great majority of species.

Differentiating characters for distinguishing the early larval stages from allied genera of Pinnotheridae are not many. As for the family, Hyman (1924) found that the minute size of the antennae in the larvae of Pinnotheridae is an important differentiating character for the larvae since the telson in some species may be normally forked and the carapace with all spines developed. As for *Pinnotheres*, Lebour (1928) has shown that the rudimentary antennae may not be an important diagnostic character (even for Pinnotheridae) as *Eballia* (*E. tuberosa*) also possesses such rudimentary antenna. According to her, larvae of British species of *Pinnotheres* (*P. pisum* and *P. veterum*) are distinguished by the telson which has three lobes.

Briefly the available information on the developmental stages of *P. latissimus*, *P. maculatus*, *P. moseri*, *P. novaezealandiae*, *P. ostreum*, *P. pisum*, *P. ridgewayi*, *P. sinensis*, *P. taylori* and *P. veterum* are given below.

Pinnotheres latissimus Burger

Miyake (1935) has described the zoeal stages of this species.

Pinnotheres novaezealandiae Filhol

Bennett (1964) has illustrated the first zoea of this species.

Pinnotheres maculatus Say

Smith, S. I. (1879) gave some notes on the larvae of *P. maculatus*.

Fish (1926) remarked that young males of *P. maculatus* were frequently seen swimming, and young stages of the species were most abundant in the plankton of the Woods Hole Region from July 6 to November 1, 1922, but subsequently in 1922 and 1923 the larvae were not present in the plankton.

According to Christensen and McDermott (1958) the figure given on Plate I, Fig. 2 as the hard stage of *P. ostreum* by Smith, S. I. (1874) should in fact refer to *P. maculatus*.

Reference is also invited to Hyman (1924) for the early stages of this species.

Pinnotheres moseri Rathbun

Goodbody (1960) reports on the greatly abbreviated development of *P. moseri* found in the atrial cavity of the simple ascidian *Ascidia nigra*. For two batches of eggs, the time between hatching and megalopa stage was found to be 24 and 36 hours and such rapid development has not been reported for other species of *Pinnotheres*. Goodbody remarks that "the significance of such abbreviation cannot be at present assessed; but it is pertinent to point out that *Ascidia nigra* is confined in its distribution to sheltered water such as enclosed bays and lagoons and is absent from communities of animals in more open areas. If *P. moseri* is an obligate commensal in *A. nigra* and cannot live in other hosts, an abbreviated larval development might be advantageous in preventing the larvae from dispersing too far away from the concentrations of its host population."

Pinnotheres ostreum Say

Birge (1882) described the first zoea of *P. ostreum*.

Hyman's (1924) description of the larval (first and second zoeas) of this species shows the trilobed condition of the telson, while the carapace is seen to be devoid of spines.

Strauber (1945) has given lengthy descriptions of the five crab stages of *P. ostreum* parasitic in *Crassostrea virginica*.

Sandoz and Hopkins (1947) based on larvae collected from the plankton in the Delaware Bay, described the development of *P. ostreum* from the egg to the first crab instar (the stages being: the first, second, third, and fourth zoea, megalopa and the first crab stage).

Christensen and McDermott (1958) have remarked on the first zoea and some of the subsequent stages of this species from Chesapeake Bay. They have classified the developmental stage of the female from the first crab stage as:

- A. First crab stage (Invasive stage).
- B. Pre-hard stage.
- C. Hard stage: Stage I.
- D. Immature female: Stage II (soft stage)
- E. Immature female: Stage III (,,)
- F. Immature female: Stage IV (,,)
- G. Mature female: Stage V

These authors have also shown that *P. ostreum* invades *C. virginica* in the first crab stage and not in the hard-shelled stage as generally believed. Theirs is the first record of the first crab stage from inside the oyster, which stage is otherwise known to be planktonic. They have also given the descriptive accounts, the habits and data on the range of carapace width of the pre-hard stages, hard stages and post-hard stages of this species, at the same time comparing the stages with those described by other workers (Strauber, 1945, Sandoz and Hopkins, 1947). They conclude that the "hard stage" earlier believed to be the invasive stage is in fact a specialised stage which "... primarily serves the purpose of uniting the two sexes for copulatory purposes. The males leave their hosts in this stage to search for females in other oysters, but this free-swimming period is only a phase in the otherwise parasitic life of the crab."

Reference has already been made elsewhere to host change associated with growth in this species reported on by McDermott (1961).

Pinnotheres pisum (Pennant)

Thompson (1835) described the first-hard shell stage of the male of *P. pisum* and this in all probability represents the earliest description of a young stage of any species of the genus *Pinnotheres*.

In a series of papers Atkins (1926, 1954 *b* and 1955 *b*) has touched upon several aspects of the development of *P. pisum*. She has shown in 1926 that the female of *P. pisum* occurs under two forms, the young female being almost indistinguishable from the male (♀ Stage-I), while the next and subsequent stages are entirely different in appearance and may be considered typically female in form. She pointed out to what is now generally agreed that the change of form between Stage I and Stage II relates to change in 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 " Later she (Atkins, 1954 *b*) gave an account of the disposition of the thoracic appendages in the megalopa of *P. pisum* when swimming. The post-embryonic development of *P. pisum* is described by her in 1955 *b*.

Lebour (1928) described and figured the prezoa and the first zoea stages of *P. pisum*.

Christensen (1959) has illustrated the first crab stage, and the pre-hard growth stage of *P. pisum*, while also discussing these and other stages of development in relation to the free-swimming habits, copulation, and host change with growth.

Pinnotheres ridgewayi Southwell

Prasad and Tampi (1959) have described and figured the zoea of this species, remarking that the zoea resembled in its general shape, telson, etc., the zoea of *P. ostreum* described by Sandoz and Hopkins (1947), but at the same time showing differences in many other respects.

Pinnotheres sinensis Shen

The developmental stages are not known; but the following information may seem pertinent. Sugaira *et al.* (1960) found in *P. sinensis* the optimum hatching season to be from September to October and from the next May to July many young crabs were found in the host and they in turn became berried in autumn. According to them "...the biological minimum size was 5.3 mm. in carapace length."

Pinnotheres taylori Rathbun

Hart (1935) described two zoeal stages, one megalopa stage, and the first young crab stage of *P. taylori*. The last said stage was found to emerge four weeks after hatching in the laboratory. She found that the megalopa of this species is easily separable from that of *P. veterum* by the presence of a small rostrum, a dorsal spine and the rudimentary sixth abdominal segment. She has suggested that when the zoea described by Aikawa (1933) as "Dissodactylozoea" and "Pinnozoea" are assigned to their correct parental species, some will be found probably to be larvae of *Pinnotheres*, and also felt that Aikawa's *Grapsizoea brevispinosa* showed superficial resemblance to *Pinnotheres taylori*.

Pinnotheres veterum Bosc

Lebour (1928) has described the first zoea, second zoea and megalopa of *P. veterum* Bosc. She has also drawn attention to an error in Gourret's (1884) work wherein figure 3 of plate 2 should refer to *Pinnotheres veterum* and figures 4 and 5 should be *Pisa*.

Atkins (1954 b) has given an account of leg disposition while swimming, in the megalopa of *P. pinnotheres* (= *P. veterum*). The post-embryonic developmental stages of this species [*P. pinnotheres* (= *P. veterum*)] are also given by her (1955 b).

3. GROWTH IN RELATION TO MOULTING

Unlike most brachyurans, moulting between copulation and egg deposition (at least four intermediate moultings in the female) occurs in *Pinnotheres* as copulation takes place when the female is in the hard shell stage. The position will be very clear from Passano's (1960) remarks, apparently based on the works of Christensen and McDermott (1958), and others. According to him "Strong metamorphic changes are relatively rare in crustacean post larval development, although comparatively minor alterations in relative growth such as the increased size of brachyuran chela... or abdomen... may be secondary sexual characters linked to the reproductive maturation." Such changes may occur abruptly at one ecdysis or more gradually during several. However, recent work has disclosed a very interesting exception in the oyster crab *Pinnotheres ostreum*. This parasite has a hard shell and appendages adapted for a free-swimming existence during the first post-larval instar, the first crab or invasive stage. After invading its host it metamorphoses into a soft-shelled stage with modified appendages. Following several moults both sexes metamorphose into a hard stage. This is characterised not only by the hardened exoskeleton, but also by a reinforced endophragmal skeleton and by appendages specialised again for swimming. The male then leaves the host, seeks out and copulates with a hard stage female in another oyster. This is the last and only sexually mature stage in the male. Fertilized female *Pinnotheres* then resumes a series of soft-shelled moults until it is fully grown.

Christensen and McDermott (1958) have given the size increases of the invasive stage, pre-hard stage, hard stage, and the post-hard stages (4 stages) of *P. ostreum*. They have also shown that growth moultings with little or no morphological changes may occur in all stages of *P. ostreum* with the exception of the invasive stage and probably also the hard stage. Nothing is known of the physiological mechanism controlling the termination of moulting of male *Pinnotheres*.

4. LONGEVITY

Upto now there is no definite information on the longevity of pea-crabs. What is known is that in a species, *P. ostreum*, the males do not develop beyond the hard stage and disappear shortly after copulation with one or more females. The observations in the laboratory carried out by Christensen and McDermott (1958) showed that all hard stage males did not survive long. However, these do not throw light on the life-span.

SEXUAL DIMORPHISM, DIMORPHIC FEMALES AND SOFT-SHELLED MALES

Sexual dimorphism is conspicuous in relation to the sizes of the respective sexes in many species of *Pinnotheres*. The males which are active and free swimming for most part are generally much smaller than the adult females which live in the host. However, in some species such as *P. pinnotheres* (Linnaeus) (= *vetrum* Bosc) no sexual dimorphism is seen and the young adult female is also capable of swimming. Dimorphism as pertaining to differences in the shape of the abdomen in the two sexes in crabs is well known. Descriptive accounts of males and females given by various workers give information on size differences.

In the early growth stages, especially in Stage I, differentiation between sexes at sight may be difficult unless the genital openings and abdominal appendages are examined. The resemblance at this stage between the sexes may be so great that in the case of *P. pisum*, Orton (1921) was misled at first to suspect protandry to be the case until he was able to obtain a female form, presumed to be a male, in which examination showed the full complement of abdominal appendages of the female. Such male-like females are recorded by Rathbun (1917) in the American species *P. maculatus*, *P. margarita* and *P. taylori*. Remarking on this and the condition obtaining in *P. pisum*, Orton (1921) observes that "These hairy male-like females are probably at first free-swimming, but after a time enter a mussel when copulation takes place."

When the male and female of *P. pisum* are seen as a pair in a host, their occurrence in relation to size and age appears to be haphazard as young males may be found with large adult females or *vice versa*, or when young pairs are present, there may be hardly any difference between the sizes of the males and the females.

Males resembling females in consistency and lack of colour have been reported by Rathbun (1918) in *P. maculatus* and Strauber (1945) in *P. ostreum*. The soft-shelled second stage males reported in the first part of this paper partly come under this category.

In the case of *P. pisum*, for a long time it was believed that males occur as one form (Atkins, 1926 a). However, in 1958 Atkins found that the male of this species occurred in two main forms, one of which approaches the young State II female in appearance. In the south-west coast of England, the latter which is seasonal in occurrence may be found from June to August. Such occurrence is also said to coincide with the occurrence of moulting stages of males and when young crabs occur in mussels and hardly ever at other times. This, as Atkins remarks, would suggest the occurrence of males in thin-shelled form during periods of rapid growth and these thin-shelled males have the normal male abdomen.

The soft-shelled male in *P. ostreum* is generally larger in size than the hard stage male and Atkins (1933), Mercier and Poisson (1929), Christensen and McDermott (1958) and others have

commented on this. Atkins has refuted a statement by Mercier and Poisson that such an unusual condition could be caused by the infestation of the crab by parasitic isopods. In the soft-shelled stage of the male (Stage II) of *Pinnotheres* sp. that we have examined there is no evidence of any parasites on the crab. According to Christensen and McDermott (1958) one plausible avenue for further investigation on this problem is whether a tendency towards protandric hermaphroditism on the part of the male crab may be involved resulting in the moulting of the hard stage male into a soft-shelled stage much resembling the second stage female. The problem may remain unsolved until an examination of the gonads of freshly caught specimens could be made.

REPRODUCTION

Some aspects of reproduction in *Pinnotheres* have been dealt with in the sections "Sexual dimorphism, Dimorphic females, soft-shelled males; Ethology—Mating behaviour," etc.

Fecundity is not known for most of the species, but available information indicates that the total number of eggs although varying within the species may also show differences from species to species. In the case of *P. ostreum*, Christensen and McDermott (1958) found ovigers measuring 9.4 and 10.8 mm. in width carrying 7957 and 9456 eggs respectively. An ovigerous female of *P. pisum* measuring 10.4 mm. in width was found by them to carry 5800 eggs. This has led them to doubt Berner's (1952) statement that *P. pisum* deposits only about 100 eggs. In the case of *Pinnotheres* sp. we have described in the earlier part of this paper six ovigerous females examined for the number of eggs have 1,700–2,800 (average 2,250) eggs.

Christensen and McDermott (1958) found that only a single batch of eggs is produced with the first spawning season in *P. ostreum*. They opine that the possibility that the crab may spawn twice during the second and twice during the third year cannot be ruled out. Thus it will be seen that there is a paucity of information in this field.

SEX RATIO

Out of 20 live *Placuna placenta* examined by them from the Gulf of Kutch, India, Hornell and Southwell (1909) found the pea-crab *P. placunae* occurring as follows:

10 individuals contained	1 female each
2 " "	1 female and 2 males each
3 " "	1 female and 1 male each
1 " "	12 males
1 " "	11 males
1 " "	3 males
2 " "	2 males each.

Southwell (1910) mentions that of 28 specimens of *Mytilus* sp. examined, 24 had one female *P. margaritiferae* each; 2 had one male and one female each; and 2 had no crabs. Ohshima (1927) remarks of a case of multiple infestation by *P. lattissimus* where 7 males were found within the shell of a *Paphia* sp. In the material (holothurians) he had examined, Chopra (1931) mentions 41 females and 3 males of *P. villosissimus*; and 11 females and one male of *P. deccanensis*.

Strauber (1945) found multiple infestation involving various combinations of crab stages of *P. ostreum* in *C. virginica*, but in no case did he find oysters with more than a single specimen of either the 3rd, 4th or 5th stage of crabs. First stage males and females were in great abundance, but the data on frequency of occurrence for 1941 and 1942 in two oyster beds he has tabulated is wanting in a sex-wise analysis of the 'Stage I crabs'. Chhapgar (1957) remarks that of 10 shells

of *Placuna placenta* opened, 4 contained a male as well as a female; 5 contained a female each and one had no crabs.

The few instances cited above indicate that the abundance of males over females may be seasonal for the species as the disparity appears most marked during the first crab stage. Besides this, on the basis of what is known no definite conclusion seems possible at this stage.

DIFFERENTIAL GROWTH IN *PINNOTHERES*

Huxley (1931, 1932) has discussed this problem in relation to the pea-crab *P. pisum*. In dealing with growth-gradients in the different regions of the body he has shown that in the abdomen of *P. pisum* the growth centre is not necessarily confined to the penultimate segment as it would appear on casual inspection, but to the terminal segment (telson) which is so small in the young female that for it to "achieve the only moderate and definitive size it must, and does, contain the growth centre."

Inspired by Huxley's preliminary observations, Williams and Needham (1935) made a study of the growth of the abdomen in *P. pisum*. The graph relating width of abdominal segment to carapace size was fitted by two successive straight lines on arithmetic graph paper, and by three such lines on log-log paper. However, instead of providing a simple method of analysis of temporal and spatial variations in the differential growth of the abdomen "... they contradicted the manifest smoothly continuous change in growth rate of abdomen relative to the carapace." They found that the growth constant was not constant even over restricted periods of growth but was a continuously variable function of carapace size giving a temporally disjointed growth picture as well as spatially disjointed into seven discrete width-measurements.

In a further study of the form transformation of the abdomen of the female *P. pisum*, Needham (1950) has elaborated on the earlier work (Williams and Needham, 1938) enabling him to give an algebraical definition of the form of the abdomen, continuous both spatially and temporally and proposes the use of the term "algebraical form—Cinematograph" for form change. These studies led him to conclude that the equation "form = shape + size," would seem to be a useful convention.

SIZE OF PEA-CRAB *VERSUS* SIZE OF HOST

The information given by some authors suggest that the crabs grow towards maturity concurrently with their hosts (Hornell and Southwell, 1909; Atkins, 1926 a; Christensen and McDermott, 1958, and others). In the case of *P. pisum* and its host *Mytilus edulis* Atkins (1926 a) has shown that a rough relationship in size between the female crabs and its host exists, the larger crabs being found in the larger mussels (e.g., crab 4.0 mm. in carapace width in mussel 41 mm. long and so on to crab 15.0 mm. in carapace width in mussel 104 mm. long). Recently, Houghton (1963) has confirmed this in his studies on *P. pisum* and *Mytilus edulis*.

Hornell and Southwell (1909) remark that immature shells of *Placuna placenta* less frequently reveal the presence of the pea-crab *Pinnotheres placuna* and in such instances the crabs were mostly immature. They opine that in this case the crabs grow towards maturity concurrently with their hosts.

Christensen and McDermott (1958) have also shown that the growth rate of *P. ostreum* from the invasive to the mature stage is positively correlated with the growth rate of the host. However, the development of the crab is not retarded in slow-growing oysters to the same extent as the rate of growth as is seen from the marked size variations of female crabs moulting into mature stage (4.4 to about 9 mm. in carapace width).

ECOLOGY

Sugiura, Kihara and Sugita (1960) found seasonal variations in the occurrence of *P. gordonii* in *Tapes japonicus*. Very low infestation was noticed from August to November when water temperature ranges from 16°-29° C., but infestation was considerably high from December-July when the water temperature ranged from 10°-26° C. In the case of *P. sinensis* infecting *Tapes japonicus*, Sugiura *et al.* (1960) found that the optimum hatching season for the species was September-October, when the water temperature ranged from 24°-19° C.

Flower and McDermott (1952-53) reporting on the heavy infestation of the Delaware Bay oysters (*C. virginica*) by *P. ostreum* remark that the crab may have less tolerance for low salinity water than the oysters.

Houghton (1963) investigated the relationship between tidal level and the occurrence of *P. pisum* in *Mytilus edulis*. The crabs were found to occur more frequently in larger mussels which were found in greater numbers lower in the shore. He found the percentage of infection to differ from one locality to another at the same tidal level and it increases from the middle shore to the sublittoral zone for any given size group. As elsewhere mentioned, he also found very low incidence of infection by *P. pisum* of mussels taken from the rafts suggesting that those near the surface of the water on floating structures are generally not infected by *P. pisum*. Houghton also found double infestation to occur in the same manner in relation to tidal level.

Depth of occurrence of some of the species of *Pinnotheres* is available from literature (Alcock, 1900; Dell, 1960; Heller, 1965; Tesch, 1918, and others). Most of the species are shallow water inhabitants found in bivalves, holothurians and ascidians. An exception seems to be *P. abyssicola* Alcock, collected from 430 fathoms from the south-west coast of India (off Travancore coast), from *Lima indica*.

Experimenting with *P. ostreum* (females of Stage V) collected from the oyster *Crassostrea virginica* close to Gloucester point, U.S.A., Nagabhusanam (1965) found that the crabs lived in salinities between 0.7 and 1.9‰ NaCl, while in freshwater they died within 24 hrs. and in salinities between 0.3 and 0.6‰ they survived for a maximum period of 3-4 days. Thus the lethal salinity was found to lie between 0.6 and 0.7‰. On the basis of this Nagabhusanam (1965) has suggested that the oysters could be protected from attacks by *P. ostreum*, if exposed to salinities of 0.6‰ or below for 4 or 5 days, the oysters not being affected as they can survive in salinities as low as 0.3‰ for as much as 15 days.

INCIDENCE OF INFESTATION BY PINNOTHERES

Strauber (1945) drew attention to the high percentage of incidence of infestation of *P. ostreum* in *Crassostrea virginica*, but was unable to explain the reasons for the unusually very high increase in the numbers of the pea-crabs in the Oysters. More than 10 small crabs per oyster were found to be present while in one oyster measuring 85 × 46 mm. as many as 262 crabs were present. For the same species collected from two localities, during different periods, Christensen and McDermott (1958) found the incidence of infestation to vary from 11.7% to 72.8%. In the sample of *Meretrix casta* examined by us as reported earlier in this paper, we found *Pinnotheres* sp. present in 48.3% of the clams. Sugiura *et al.* (1960 a, 1960 b) have given information of the incidence of infestation of *P. sinensis* and *P. gordonii* in *Tapes japonicus*.

ETHOLOGY

Ethology is defined as 'the science of character' and would broadly imply an approach in the study of animal behaviour. Thorpe (1958) speaks of three scientific ways of probing into

the behaviour of animals, namely "... the way of the naturalist, the way of the psychologist, the way of the physiologist." In the case of the pea-crabs of the genus *Pinnotheres*, what little information available on the subject of ethology is to be found under the first and the last categories mentioned above. A resume of this is given below under suitable subheadings.

1. PHYSIOLOGY OF COMMENSALISM WITH SPECIAL REFERENCE TO PEA-CRABS

Recent years have found more emphasis placed on studies relating to the physiology of commensalism, especially the role of specific chemical factors controlling host commensal relationships, which is an important aspect of ethological studies. Some notable contributions touching on this field—physiology of commensalism—are by Bartel and Davenport (1956), Caullery (1952), Dale (1957), Davenport (1950, 1953 a, 1953 b, 1955, 1960), Davenport, Camongis and Hickock (1960), Davenport and Hickock (1951), Hickock and Davenport (1957), Hodgson (1955), Johnson (1952), Mansueti (1963), Sastry and Menzel (1962), Thorape and Jones (1937), Welsh (1930, 1931), and others. All these works do not directly pertain to studies on behaviour of pea-crabs, but touch on important aspects of such studies which may also have to be extended to pea-crabs for a proper understanding of their behaviour patterns.

In a series of papers mentioned above, Davenport and collaborators have tried to demonstrate in host-commensal associations to be found in the marine environment, whether or not there is any chemical bond existing between host and the partner. Although excellent biological studies on species of *Pinnotheres* and their host species are available, hardly anything is known about the factors which attract these crabs to their hosts. In the case of pea-crabs this is very significant as the crab enters a host during the invasive stage, when there is a host change during growth, and when the male moves about from host to host in search of the female of the species for mating. It is not known that if there be any chemical attractant to attract the commensal to its host, whether this would be present throughout the adult part of the life-span of the host or restricted to seasons or to only a particular time during its adult life-span. Whether the commensal evinces any 'territorial behaviour' namely the capability to drive away any intruders or whether the host could expel the commensals at will is not well understood. Whether the reported cases of parasitism by the pea-crabs in oysters, mussels, and clams take place at a time when already the host is not "in condition" being affected by other parasites such as heavy infestation of oysters by cercariae is not known. This is of importance where mortality of the pea-crab infested host takes place.

In a species of an allied genus of *Pinnotheres*, namely *Dissodactylus*, Johnson (1952) has demonstrated by the use of Y-tube choice apparatus that water from an aquarium containing the host sand dollar *Mellitia* has a strong attraction for the crabs, and as pointed out by Davenport (1955), that this is the first time that such a chemotaxis has been demonstrated in Pinnotherids, though one has long suspected as a result of their habit that such a response could be shown. The specific factors for bringing about this response in *Dissodactylus* is not known. Johnson's work on two other pea-crabs commensal with the polychaete *Chaetopterus* and the oyster crab commensal with *Ostrea*, however, did not result in the crabs demonstrating any positive response as in the case of *Dissodactylus*. Whether closer contact with the host could have elicited any recognition response was not demonstrated.

In this connection the work of Sastry and Menzel (1962) dealing with host recognition of *Pinnotheres maculatus* already referred to under the section 'Host specificity' needs special mention. They found that *P. maculatus* is capable of recognising its hosts *Aequipecten irradians concentricus*, and *Atrina rigida* under experimental conditions described by them. They deduce that some unknown attractant from the hosts is responsible for the active movements of the crabs in the presence of the hosts, and such stimulated movements depended on the proximity of the hosts. They opine that the decreased attraction could result either from a gradient or the highly diffusible nature of the attractant. That the attractant could emanate only from the soft parts of the scallop is evident from their experiments as the crabs showed no attraction or response towards empty shells

attached with epizooites. Another interesting result of their work was the finding that both males and females of *P. maculatus* were equally responsive to their host scallops.

On the whole it will be seen that even the fringe of this problem has not been tackled as innumerable associations involving pea-crabs and their host bivalves, holothurians, ascidians, etc. remain yet to be investigated. Problems such as how from the free living early stage the pea-crab changes to a commensal habit may remain unanswered for a long time to come. However, the finding that *Pinnotheres* is hardy enough to survive in the laboratory for experimentation for physiological and behaviour studies is heartening.

2. PHOTOTROPISM OF LARVAE OF *Pinnotheres* UNDER LABORATORY CONDITIONS

The first zoeal stage of *P. ostreum* was found to exhibit a distinct positive phototropism in the laboratory (Christensen and McDermott, 1958). This is in agreement of Lebour's (1928) observations on newly hatched larvae of *P. pisum* which were found at first to rise to the surface, but soon descend to the bottom when they feed. Welsch (1932) reported zoea of *P. maculatus* seeking the bottom three to five days after hatching the Miyaki (1935) found that zoea of *P. latissimus* doing likewise even one or two days after hatching.

In this connection it may be mentioned that Lebour (1928) has suggested that the form of the telson in the zoea of *Pinnotheres* may be an adaptive feature enabling the zoea to descend and remain close to the bottom. The telson at this stage is flat, plate-like and not forked and possesses only short spines and this condition may help the larva to curl up its body. The similar habit of curling up the abdomen under the body so as to form a ball is also reported in the case of *P. ridgewayi* by Prasad and Tampi (1959).

3. COLOUR CHANGE IN *Pinnotheres*

Atkins (1926 b) reports of some observations she made on colour change in two specimens of *P. veterum* from the branchial chamber of *Ascidia mentula*. At night, activity in the dark was accompanied in the male by the loss of colour. The female which had no definite colour pattern showed no appreciable change. "The male was golden brown, shaded with dark brown, the colour being due to orange and dark brown chromatophores, now fully expanded and their pigment diffused. In the dark it became pallid and transparent, some faint yellow diffuse pigment only being visible; the gut contents showed black, the testes white. This loss of colour is due to the reaction of the pigment in the chromatophores induced by the onset of darkness. Of the two pigments the orange had the quicker rate of flow and is probably lodged in a smaller cell." Atkins also found that when the crabs were placed in the dark during day, they sometimes reacted as at night taking 40-60 minutes to do so. When uncovered, the males took about the same time to recover.

4. EFFECTS OF TEMPERATURE AND LIGHT ON MOVEMENTS OF LARVAE OF *Pinnotheres*

Welsh (1932) found that temperature and light were important factors in determining the locomotions of larvae of *P. maculatus*. He observed velocities over the range 13.4°-27.0° C. in the directional light of constant intensity and also over a range of intensities from 0.093-93.0 meter candles at constant temperatures indicating that the velocity of progression was related to the light intensity according to the expression:

$$\log V = K \log I - C.$$

This treatment yielded rectilinear graphs which were convenient for comparing effects of temperature and intensity of illumination,

5. REACTION OF *Pinnotheres* TO ANAEROBIC CONDITIONS IN THE HOST

In the course of his work on *Pinnotheres pisum*, Berner (1952) found that mussels subjected to prolonged desiccation at the upper tidal limits were devoid of pea-crabs. He felt that the anaerobic conditions within the mantle cavity of such mussels during their exposure could be a possible explanation. Other factors, such as depth of water in such beds during high tide, flow of water (currents in the beds), frequency and duration of exposures all have a bearing as to whether or not the invasive stage will be able to settle and invade the host. As discussed elsewhere (*vide infra*) the feeding behaviour of the crabs may also preclude to a great extent crabs infesting oysters in such exposed beds.

In this connection, the general non-occurrence of pea-crabs in mussels attached to submerged floating objects (rafts) drawn attention to by Houghton (1963) perhaps needs some other explanation for which the behaviour of the crab at the invasive and post-invasive stages may also have to be taken into account.

6. FEEDING BEHAVIOUR

Orton (1921), Strauber (1945), and others have made direct observations on the feeding behaviour of species of *Pinnotheres* within mantle cavity of the host bivalves. MacGinitie and MacGinitie (1949) by putting a glass window in the shell of a mussel were able to watch the activities of the pea-crab *Pinnotheres concharum* (= should be *Fabia subquadrata*, closely allied to *Pinnotheres*). The crab was found to obtain its food by eating some of the mucous strings by means of which the mussel carried its food to its mouth.

Orton (1921) found *P. pisum* pick up food strings from the margins of the gills of the host with the chelipeds. Strauber (1945) has given details of the mode of feeding of *P. ostreum* in *Crassostrea virginica* and the disposition or orientation of the crab within the oyster at the time of feeding. He found considerable similarities in the feeding of *P. pisum* in *Mytilus edulis* reported by Orton, and his own observations.

There is strong evidence that some species of *Pinnotheres*, especially those living in the excurrent region of the atrial cavity of tunicates such as *P. pugettensis*, *P. taylori*, *P. pinnotheres*, etc., resort to filter feeding (Welsh, 1940). This mode of feeding is also likely to occur in the earlier post-invasive stages. This is evident as large numbers of immature *P. ostreum* found in the mantle cavity of *Crassostrea virginica* appear not to cause any damage to the host. The pre-invasive stages depend on filter feeding. White (1937) remarks that the stomach of *P. pisum* has been found to contain diatoms and other food substances of the mussel. Coupin (1894) found this species to feed on food filtered from the water by the host mussel.

The mode of feeding thus is likely to change with growth, and this may partly account for damages seen in the tissues of the host when it harbours larger crabs. It is also possible that the smaller pea-crabs resort to both filter feeding and picking up food particles from the mucous strings formed along the margins of the gills of the host. Thus, the feeding behaviour at the different stages may restrict the number of crabs in a host as they have to depend on the amount of food brought into the oyster per time unit, and the young which may resort to also filter feeding more so. These considerations have led Christensen and McDermott (1958) to suggest the possibility that differences in survival of oyster crabs invading spat and older oysters may be due to difference in the amount of water pumped by the host animal. This may also thus account for the absence of crabs in oysters found in beds liable to be frequently exposed.

7. MATING BEHAVIOUR

Atkins (1926 a) has shown that *P. pisum* is peculiar in copulating precociously at an extremely early stage, and suggests that in all probability the sperm from the first copulation is sufficient to

fertilise several batches of eggs. However, the occurrence of occasional adult females with empty spermathecae suggests the possibility that copulation may take place more than once. Earlier, Orton (1921) found that in *P. pisum* copulation normally took place inside the host, and males visit mussels in search of females. He also found a hard stage female with its spermathecae filled with mature sperms indicating thereby the early stage at which the crabs copulate.

Strauber (1945) doubted the possibility of copulation of males and females differing too much in size in *P. ostreum*. Conclusive evidence is wanting as to the copulation of hard stage males with Stage V females in *P. pisum*, although reported on by Berner (1952). The possibility that crabs which became ovigerous in the laboratory tanks may already have had sperm in the spermathecae when they were collected cannot be overlooked in this case although Berner observed the male and female together. In the laboratory tanks, Christensen and McDermott (1958) have also observed a hard stage male with its pleopods extended enclosed under the abdomen of a Stage V female. However, they are not sure whether actual copulation took place or not.

As reported in the first part of this paper, in the case of *Pinnotheres* sp. infesting *Meretrix casta* we have found a number of instances of hard stage males with Stage V ovigerous females and one possible explanation may be that the males in search of hard stage females had entered the clams with the ovigerous females. The occurrence of several hard stage males and ovigerous females singly in clams may add weight to this explanation.

The problem thus revolves round the question whether the hard stage males effectively copulate with the Stage V females or only with the hard stage females. While the latter condition is the rule, the former is suspected in species evincing disparity in sizes of the sexes. Nothing appears to be known about this in species in which adult males and females are of about the same size.

8. FREE-LIVING HABIT OF ADULT FEMALE *Pinnotheres*

Adult females (Stage V) are not known to occur outside their hosts, and there is no definite information about their moving from host to host, especially as the body form is not suited for free-living. In this connection, the work of Sugiura *et al.* (1960) is of interest as they found that female *Pinnotheres sinensis* could live free from its host *Tapes japonicus* for as much as four to six months in the laboratory aquaria.

9. BEHAVIOUR OF PEA-CRABS IN PRESENCE OF ANEMONES

Plessis (1954) has noted the behaviour of *P. pisum* kept in an aquarium along with anemones.

HOST SPECIFICITY

A large number of works dealing with the original descriptions of species or mere distributional records of pea-crabs of the genus *Pinnotheres* unfortunately do not throw light on the specific identity of the host species other than mention the host as a bivalve, a holothurian, an ascidian or give only the generic identification (*e.g.*, *Donas* sp.). This is an unsatisfactory state of affairs which will not permit even a gross appraisal as to whether species or species groups show any preference to particular host or host groups. However, in the case of a few species, such as *P. ostreum*, *P. pisum*, *P. gordonii*, etc., we have more definite host identifications. The last said species from Japan is said to occur in six species of bivalves [*Tapes japonicus*, *Mytilus edulis*, *Ostrea (Crassostrea) gigas*, *Meretrix lusoria*, *Macra veneriformis* and *Chlamys nipponensis*] and one gastropod [*Umbonium (Suchium) moniliferum*] (Sugiura *et al.*, 1961). It should be mentioned here that the occurrence of a pea-crab in a gastropod is most unusual,

At the same time, a species showing a more extensive distribution as *P. pisum* in the Atlantic and Mediterranean is known from fewer hosts, all bivalves. A careful scrutiny of the known host records of the different species of *Pinnotheres* indicates that generally a species commensal in a bivalve is not met with also in a holothurian or an ascidian. As to what extent this would reflect our ignorance of all the natural hosts of the known species of pea-crabs is difficult to say at this stage. Similarly the correct identification of the crab species itself may stand in the way of a proper assessment. We have mentioned this to draw attention to the lacunae which needs filling.

Experimental studies on host specificity is a relatively new field of investigation and in the case of pea-crabs we have at least one instance in the work of Sastry and Menzel (1962) wherein they have shown that *Pinnotheres maculatus* commensal on the bay scallop *Aequipecten irradians concentricus* and the pen-shell *Atrina rigida* (from Alligator Harbour, Franklin County, Florida) did not show preference for one host over the other. In fact, the crabs removed from the scallops and experimented appeared to be non-host specific.

Similarly, in places where more than one species of bivalve is present in an area, it is not known whether and if so to what extent the pea-crab could evince host specificity. The collections of the same species of *Pinnotheres* in a particular area from more than one host species no doubt indicates the non-host specific nature of the crab. However, before arriving hastily at this conclusion one factor dealt with below has to be thought about. Such an interesting situation while studying host specificity arises in instances where host change occurs at different stages of growth of the crab. One such instance of definite host change in relation to the growth stage of the pea-crab is reported by Christensen (1959) in the case of *P. pisum*. He obtained the different progressive growth stages from two hosts from the same area, namely *Spisula solida* harbouring the invasive and first crab stage and *Modiolus modiolus* the hard-shelled stage and subsequent stages. Examining specimens of both the host species from the same dredge haul he remarks that "... it was found that 21 *Modiolus* contained 10 hard-shelled stage, 2 Stage IV and 5 Stage V crabs but no invasive or small soft-shelled specimens, while 38 *Spisula* contained 5 first crab stages varying in size from about 0.70 to about 0.75 mm. and 5 hard-shelled crabs (Stage I)."

A parallel instance is that of *P. ostreum* drawn attention to by McDermott (1961). This species matures and becomes ovigerous in *Anomia simplex* whereas in *Mytilus edulis* they develop only to hard swimming stage. According to him, in the Jersey area of the east coast of U.S.A., *P. ostreum* leaves the mussels at the attainment of the hard swimming stage during the late fall apparently in search of some other host and mature females have not been found in mussels.

In instances such as those mentioned above where host change of the crab occur with growth and consequently two host species are needed for the successful completion of the life-history of the commensal species it will not be wrong to say that the crab shows host specificity to two species. The possibility that the pea-crab could be host specific at one phase of its growth, but not at another cannot also be ruled out. The problem needs special attention.

Among the Indian species of *Pinnotheres* one species, *P. placuane*, has a markedly dorso-ventrally flattened body with a more or less squarish carapace to enable it to live in its host, the greatly flattened window-pane oyster *Placuna placenta*. In view of the adaptive modifications seen in this pea-crab, it can be safely stated that it is host specific.

EFFECT OF INFESTATION BY THE PEA-CRAB ON THE HOST

The species of the genus *Pinnotheres* have a wide variety of hosts, but up to now the activities of the crabs bordering on parasitism or actually being parasitic has been reported only in the case of bivalves harbouring them. Hale (1927) cites a statement that *Pinnotheres subglobosa*

(= *Ostracotheres subglobosa*?) from South Australia known to infect at least three bivalves, *Chlamys bifrons*, *Spondylus tenellus* and *Modiolaria australis* is apparently "deeper sunk in parasitism than other members of the genus." In the case of at least one species it has been shown that the physical damages it causes to the host tissues may lead to mortality of the host. Indirect effects on the host, such as hermaphroditism have also been attributed to the pea-crab and these are dealt with below.

1. "INDEX OF CONDITION" OF INFESTED OYSTERS

Sandoz and Hopkins (1947) found *Crassostrea virginica* to show poor condition when infested with *P. ostreum*, than when uninfested. However, exceptions of crab infested oysters showing excellent condition were also seen by them. They found that mortality of oysters on account of pea-crab infection did not occur in Virginia as in New Jersey (Strauber, 1945), although incidence of crabs was noticed. They remark that "Miss Alice Elizabeth Overcash, in an unpublished thesis, 1946... has studied the "Index of Condition" of Virginia oysters, including many with oyster crabs. She reports that this index:

$$\frac{(1000 \times \text{dry weight of meat in gm.})}{\text{Volume of shell cavity in milliliters}}$$

averaged only 82.3 for the crab-infested oysters in New York River, compared to 90.6 for oysters without crabs. In Rappahannock River she found the mean index of oysters with crabs to be only 71.7, while the entire sample averaged 90.0. Both samples show significantly poor condition in infested oysters.

Christensen and McDermott (1958) found that oysters showing extreme cases of gill erosion were found to be in very poor condition. However, they feel that there is no conclusive evidence of possible differences in shell thickness or weight of living tissue in relation to infestation. This led them to conclude that only the presence of mature crab over a longer period of time will noticeably affect the growth of the host under normal environmental conditions.

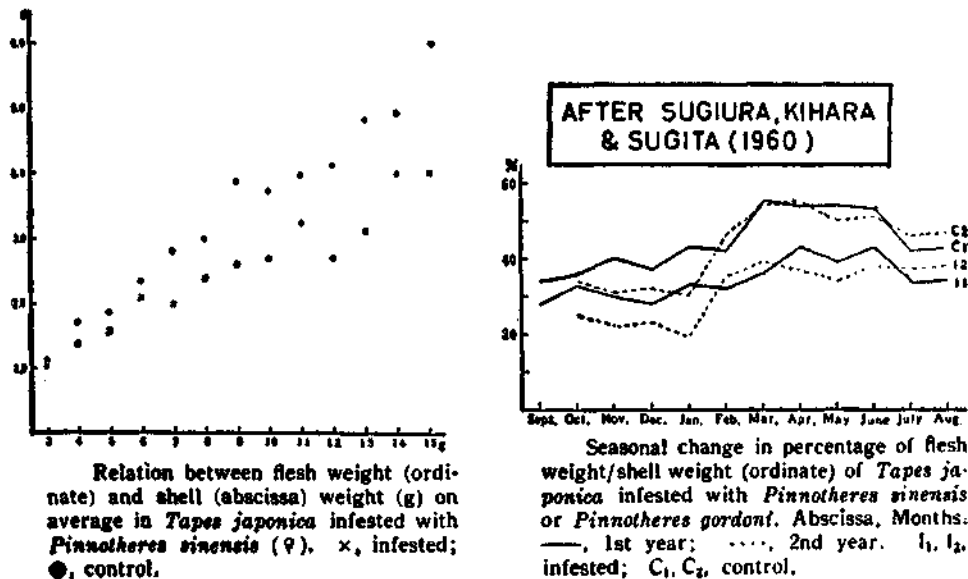
Sugiura, Sugita and Kihara (1960) found that *Tapes japonicus* infested with *Pinnotheres sinensis* was lean without regard to their size or season. In the case of *P. gordonii* found also infesting the same host, they (Sugiura, Kihara and Sugita, 1960) found certain amount of damages caused by the pea-crabs. Using the formula $W \times 100/sw$, where W = total weight of flesh of clam; and sw = shell weight of it, uninfested clams gave a value of $49.8 \pm 12.1\%$ and infested clams $41.6 \pm 12.6\%$. This as well as the graphs they have given for flesh weight/shell weight of *Tapes japonicus* infested and uninfested with *P. sinensis* and *P. gordonii* have been reproduced here to facilitate reference and to clearly show the effect of the infestation (Text-Fig. 4).

In our observations on *Pinnotheres* sp., infesting *Meretrix casta* we found no significant difference in the meat weight/total weight ratio and have given possible reasons for this.

2. DAMAGES CAUSED TO THE GILLS OF THE HOST

Strauber (1945) described two types of gill damages caused by *P. ostreum* to *C. virginica*; "the small-crab type with a local, sharply delimited erosion of one or more demibranchs, and the large-crab type where an extensive shortening of one or more demibranchs may be seen reaching from the anterior end of the gills to a point usually ventral to the adductor muscles." Christensen and McDermott (1958) found in *C. virginica* infested by *P. ostreum* after examining 1502 oysters that nearly all oysters infested showed some gill damage: 50% had light gill damage, about 40% had moderate gill damage, and about 9% had heavy gill damage and only 1% had no discernible gill damage. This led them to conclude that gill damage or gill erosion gradually develops from the

first type to the next. They also found that among older oysters a few extreme cases of heavy gill damage where there was hardly anything left of the gills were present, and that these were in very poor condition. Strauber (1945) has also remarked on instances of gill regeneration. He is of the opinion that the gill damaged oysters lose their crabs at times or they eject the dead crabs. Regeneration of the essential gill structure may take place after this, but the scar mark will be still evident at the place of original damage. There is hardly any study on the histological aspects of the healing process in once parasitised oysters or other bivalves.



TEXT-FIG. 4. Relation between meat weight and shell weight in the Japanese clam *Tapes japonica* infested with *Pinnotheres sinensis* and *P. gordonii* and in control samples (after Sugiura, Kihara and Sugita, 1960).

McDermott (1962) found gill damage in *Mytilus* caused by *P. maculatus* and *P. ostreum*, but the latter species when found in *Anomia simplex* did very little damage to the gills of this species.

Sandoz and Hopkins (1947), and Flower and McDermott (1952-53) have shown that heavy infestation of the oysters by *P. ostreum* produced gill erosions of the host in varying degrees. We have elsewhere in this paper shown the various types of gill erosion seen in *Meretrix casta* caused by *Pinnotheres* sp.

3. DAMAGES CAUSED TO THE PALPS OF THE HOST BIVALVES

Strauber (1945), Christensen and McDermott (1958) and others have mentioned that pea-crabs cause damage to the palps of the host also. McDermott (1962) found palp erosion in *Mytilus* caused by *P. maculatus* and *P. ostreum* and pointed out that the palp abnormalities in *Mytilus* reported by Atkins (1931) might also have been caused by pea-crabs.

4. EFFECTS ON REPRODUCTION OF HOST BIVALVES—HERMAPHRODITISM AND OTHER ANOMALIES

Awati and Rai (1931) attributed the change of sex of the Bombay oyster (*O. cucullata*) partly due to the infestation of a pea-crab, *Pinnotheres* sp. In this connection the following details are given by them;

Sex of animals harbouring pea-crabs	Numbers examined	Percentage
Male ..	71	82.56
Female ..	9	10.46
Hermaphrodite ..	6	6.97
Total ..	86	

They remark that "The very large proportion of males against females amongst oysters harbouring the pea-crab is remarkable. Ordinarily the proportion of males and females is almost equal, while the existence of the hermaphroditic individuals is almost negligible amongst oysters without the pea-crabs..." This they deduce from the data they have given which is reproduced below:

Sex	Numbers counted	Percentage
Male ..	326	41.7
Female ..	445	56.4
Hermaphrodite ..	23	2.9
Total ..	794	

No information is available from their work as to the stages of the pea-crabs they found infesting the oysters, the sex-wise ratio, etc. It is interesting that Durve (1960) studying the Bombay oyster *Crassostrea gryphoides* found only 5 out of 3,000 examined by him containing one each of a pea-crab (*Pinnotheres* sp.).

Amemiya (1929) and Coe (1934) have shown that *Crassostrea* has a strong tendency towards protandric hermaphroditism and the sex ratio in this oyster is definitely influenced by environmental conditions. Experimental works on removal of parts of the gill tissue in *Crassostrea gigas* carried out by Amemiya (1935), and Egami (1953) have shown the increase in the proportion of males to females during the breeding season when the operations are performed "... no later than the previous October." To elaborate, Egami's (1953) studies on the sexuality of this Japanese oyster after removal of gills indicate that animals in a state of undistinguishable sexuality (those which have passed one winter) from which gills were removed in October 1951 (October 21 and 22) and January 1952 showed the following results: the Proportion of males in the breeding season is definitely larger in the group from which the gill tissue had been removed in the October batch than in the control. However, no appreciable changes in the sex ratio between the controls and those operated on in January were noticeable. The results indicate the role played by environmental conditions in controlling the sex-phase of the Japanese oyster. This we mention here especially to lay stress on the significance of gill erosion in oysters and other bivalves caused by the pea-crabs and the indirect effect this could have on the sex-phase of the host.

In the case of the mussel, *Mytilus edulis*, Berner (1952) found that the gonads of individuals parasitised by large specimens of *P. pisum* are functionally inhibited without showing visible signs of atrophy. He found on examining over 300 mussels thus infected that those having crabs measuring 10 mm. or more in carapace width showed partial or even complete cessation in the production of sexual products, while those harbouring smaller pea-crabs were hardly affected. His

interpretation was that the crabs which caused these changes in the host were in their second and third year. This finds favour with Christensen and McDermott (1958) who suggest that the reproductive system in *Crassostrea virginica* may similarly be affected by *P. ostreum* "...atleast in the second spawning season in which it harbours the same crab, i.e., yearling oysters are probably never affected."

5. OTHER EFFECTS ON HOST BIVALVES

White (1937) speaking of the 'apparently harmless' association between *P. pisum* and its host *Mytilus edulis* remarks that larger crabs may exert pressure on various organs of the host, especially the mantle and subscribes to the view that the damaged mantle by its pathogenic secretions may cause the wearing away of the nacreous layer of the shell.

Young (1960) mentions that the picking off of mucous laden strings of food by the pea-crab would affect both the food and feeding efficiency of the host, although the pea-crab may not cause any deliberate damage to the host tissues.

Some of the damage caused by the pea-crab to its host has been attributed to the friction caused by the hard and unyielding exoskeleton of the first stage crab on the soft parts of the host.

A characteristic irritating flavour in the Madagascar oyster, *Ostrea vitrefacta* was linked with the presence in this oyster of a species of *Pinnotheres*, by Poisson (1946). Further he associated the presence of *Sertularia* often found on the shells of oysters containing *Pinnotheres* and the attacks of nettle rash of people consuming oysters with such association. According to Korringa (1955), this information corresponds to the belief in Holland that *P. pisum* is responsible for bringing about nettle rash, in those who consume the mussel, *Mytilus edulis*. He concludes that no special flavour has been noticed in mussels containing *Pinnotheres* and there is no justification for assuming that *Pinnotheres* has anything to do with the allergic reaction in some people seen after eating mussels. However, it would be "interesting to hear about possible associations of *Pinnotheres*, irritating flavour and nettle rash in other species of oysters." To our knowledge such information is wanting.

PARASITES OF SPECIES OF THE GENUS *PINNOTHERES*

In his account on "Challenging problems in shellfish biology" Loosanoff (1958) mentions that the successful control of oyster enemies such as starfish, gastropods, crabs, etc., 'is extremely difficult and often impossible'. Biological control is a possibility, but has not been tried, nor will it be in the foreseeable future. Through the excellent works of Atkins and others it is known that *Pinnotheres* itself may be subjected to attacks by isopod parasites, certain saprolegniaceae, and rhizocephalans, some of which may cause death to the host crab.

1. ISOPOD PARASITES OF *Pinnotheres*

Giard and Bonnier (1899) reported briefly with illustrations a new genus and species of Entoniscidae, *Pinnotherion vermiformae* which they found infesting a *Pinnotheres* inhabiting *Modiolus modiolus* at Dimereaux (Belgium). They remarked that the host pea-crab was not *Pinnotheres veterum*. Bonnier (1900) later gave the host identification as *P. pisum* without adding further details to the description of *Pinnotherion vermiformae*. Mercier and Poisson (1929) found this parasite infecting *P. pisum* at Luc-sur-mer. Atkins (1933) found it on *P. pisum* inhabiting *Mytilus* in the estuary of Camel, North Cornwall. She discovered that the male of *P. vermiformae* may occur as an internal parasite and also showed that the percentage of infestation with this species (*P. vermiformae*) was greater in female *P. pisum* (31.8% or 129 out of 415 specimens examined and 3.45% or 2 out of 58 in males examined). 28.69% of *P. pisum* were found to be infected

with one or more specimens of *P. vermiformae* and on the whole male *P. vermiformae* were found to be more common in occurrence (26.85%) than the female parasites. Mercier and Poisson (1929) found that *Pinnotherion* infected 9% of females and 1.5% of males of *Pinnotheres*. Such occurrence was explained even earlier by Bonnier (1900) who noticed this frequency of occurrence and by Mercier and Poisson (1929) as being due to fewer males than females of *P. pisum* being present in their host *Mytilus*. Atkins (1933) has drawn attention to another possibility, namely the relative thickness of the carapace of the male and female *P. pisum* as an important factor affecting the incidence of infestation in both sexes. Bonnier (1900) has shown that infestation with epicarid isopods appears to be heavier in some years than in others. According to Atkins (1933) the presence of adult *Pinnotherion vermiformae* in *P. pisum* would seem to cause partial or complete atrophy of the gonads.

Giard and Bonnier (1887) have noted for other Entoniscidae as well as for *P. vermiformae* (in 1889), that the hepatopancreas (liver) of the host *P. pisum* are much reduced, the parasite occupying almost all the available space.

Whether female *Pinnotherion* prevents moulting of the host *P. pisum* is not known, but Atkins (1933) opines that this seems probable.

The presence of dead or degenerating male *P. vermiformae* have been found in different parts of the body of the host attached to the lobes of the hepatopancreas, or embedded in the gonads, thorax, or abdomen as small yellowish oval masses. Atkins (1933) presumes that these males would have died in an attempt to moult as the position of the abdomen suggest "... except in one case when there seems to be an attempt on the part of the host to surround the male."

Hale (1927) reports that one specimen of *Pinnotheres subglobosa* (Baker) (= *Ostracotheres subglobosa*?) taken from the bivalve *Chlamys* had a large parasitic isopod (Epicarid) beneath its abdomen.

2. SACCULATION IN *Pinnotheres*

Boschma (1953) described a new rhizocephalan, *Sacculina pertenuis* from a species of *Pinnotheres* taken at Gulf of Suez.

Sacculinization and sex differentiation were reported on by Semitu (1944) in *Pinnotheres cyclinus* and *P. sinensis*. According to him, the secondary male characters of these species turn female-like as a result of sacculinization, but the female secondary sexual characters and the ovary are scarcely affected. The actual changes in the parasitised male are the appearance in the middle part of the testes pseudo-egg cells derived from the primordial germ cells. The latter are accompanied by a few follicle cells, but are devoid of yolk and reduction division is not seen. The spermatocytes are located round the pseudo-egg cells which occur as groups or clusters in the spermatogonium stage. As the change of the secondary male characters is always brought about even if the testes is completely degenerated by sacculinization, Semitu (1944) is of the opinion that some other phenomenon which cannot be explained endocrinologically is at work in addition to the function of the sexual hormone.

3. BARNACLES AND OTHER ORGANISMS FASTENED TO *Pinnotheres*

Strictly speaking the information given here will not come under parasitism, but this appears to be an appropriate place for mentioning this. Ryder (1882) remarking on Protozoa and Protophytes as direct source of food of fish mentions of an instance of multiple parasitism involving also a *Pinnotheres* as "On another occasion I found something like *Poteriendron* on the *Zoothamnium* which covered a *Pinnotheres* inhabiting an oyster; but the chain of parasitism did not stop here, for on the monad, as well as on the bell-animal, there were rod-like bodies attached which were

presumably bacteroid..." A similar observation by Hale (1927) bears citing here. He "...on removing a pea-crab from *Spondylus*, discovered that a parasitic barnacle (Rhizocephalid) was attached to the pleon of the crab, and that a parasitic isopod (Epicarid) was fastened to the barnacle. In this remarkable case we have a tiny, malformed isopod feeding upon a degenerate barnacle, which in turn is drawing its nourishment from the soft-shelled little crab which relies upon a mollusc for shelter and food."

Hale (1927) also mentions of a specimen of parasitic barnacle taken from beneath the abdomen of the pea-crab *P. holothuriensis* (= *Ostracotheres holothuriensis*?) from Edithburg, South Australia.

4. INFECTION OF SPECIES OF *Pinnotheres* BY MARINE FUNGI (SAPROLEGNIACEAE)

Three species of marine fungi, *Leptolegnia marina*, *Plectospora dubia* and *Pythium thalassium*, have been described by Atkins (1929, 1954 a, 1954 c, 1955 a) from *P. pisum* and the first mentioned species also doubtfully from *P. pinnotheres* (= *veterum*), from British waters.

Leptolegnia marina was described from *P. pisum* taken from *Mytilus edulis*. The fungus penetrates deep into the body of the pea-crab surrounding the organs, and generally the gills, and may also extend into the appendages, mouthparts and even eye-stalks. Atkins (1954 a) found that the duration from the onset of the infection to the death of the crab was highly variable, and under laboratory conditions this was found to vary from 8-57 days and in one exception the crab died on the 78th day. More females than males of *P. pisum* were found to be infected with *L. marina* but this could have been due to the fact that more female crabs than males were examined. The infection was also seen in the eggs as well as embryos of *P. pisum*.

External growth of the fungus was not seen in dead infected crabs left in the sea-water. Regarding this Atkins (1929) says that the apparent inability of this fungus "...to form a growth on dead crabs may seem to argue in favour of its truly parasitic nature, but putrefaction of *Pinnotheres* is somewhat rapid and it may be that the number of bacteria, etc., present, check the growth of the fungus and kill it." Atkins (1929) concluded that *P. pisum* infected with this fungus always dies, but definite evidence as to whether the fungus is pathogenic or only invades tissues which have been destroyed by parasitic bacteria is wanting. The data she gives of mortality of pea-crabs infected with fungus when kept together in bowls, and individual crabs kept in separate bowls indicate low mortality rate for the latter while very high mortality rate was seen in the former kept in batches varying from 5-21 specimens. This would suggest that the disease is extremely infectious.

As regards the lone instance of the occurrence of *L. marina* on *Pinnotheres pinnotheres*, Atkins (1954 a) remarks that this was found on a tiny male (2.1 mm. in carapace width) "...obtained on 15th March 1928 from Teignmoth and found dead on 4th May with the fungus visible on the walking legs. It most probably became infected in the laboratory."

Plectospora dubia was described by Atkins (1954 c) from the eggs of *P. pisum*. The infected eggs showed a greater development of the space between the inner and outer egg membranes caused by the growth of the fungus. Such eggs showed a greater diameter (about 0.5 mm.) than the healthy eggs (0.33 mm.). The gills of the pea-crabs were found to be unaffected.

Pythium thalassium was also described by Atkins (1955 a) infecting the eggs of *P. pisum* and other crustaceans.

REACTIONS OF THE HOST BIVALVES TO INVASION BY PEA-CRABS

In a review of this nature it is equally important to consider the reaction by the host animal to invasion by the commensal. At the outset it should be mentioned that the available information is scanty, but we have given below the relevant observations we are able to glean from literature.

It is generally believed that the crab being a commensal the partnership is one of mutual concord. However, a few instances have been reported where this is not the case. Strauber (1945) found that invasion of older oysters (*C. virginica*) by the hard-stage crabs of *P. ostreum* is always not easily accomplished. The larger oysters may expel a number of tiny invasive stages of the crab by enveloping them in mucous and by passing them out by ciliary action and clamping the valves.

Atkins (1955) observed the expulsion of megalopa of *Pinnotheres pinnotheres* inserted in *Mytilus edulis*. Some observations made by Strauber (1945) on the mode of infestation of *C. virginica* by *P. ostreum* indicates that the pea-crabs which have not effected complete entry are liable to be crushed or trapped due to the clapping of the valves. He agrees with Orton's (1921) view that although the hard flat shell of the invasive first stage of the pea-crab has an adaptive value in allowing the crab to slip within the valves of the mollusc and also in avoiding crushing by the closing valves, experiments carried out indicated that successful invasion did not always occur.

In *P. pisum*, Orton (1921) remarks that "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 extraordinary strong carapaces and creep inside the mussel later when it must perforce relax and open its shell in order to breath."

Woodward (1886) remarked on a very interesting instance of a male *Pinnotheres* being encysted in the nacreous layer of the pearl oyster *Meleagrina margaritifera* suggesting that the animal had "... intruded at an unfortunate time, when no female of his kind happened to be in, and that having penetrated too far beneath the mantle in the ardour of his search was made prisoner before he could escape." This instance is also cited by Cooke (1959).

III. TAXONOMY, NOMENCLATURE, SPATIAL DISTRIBUTION AND HOST RECORDS OF SPECIES OF THE GENUS *PINNOTHERES*

TAXONOMY AND NOMENCLATURE

Alcock (1900) provisionally subdivided the family Pinnotheridae into four subfamilies which are recognised by later workers (Tesch, 1918; Sakai, 1935). These subdivisions are, subfamily Pinnotherinae Alcock with the following genera recognised by Tesch (1918) under it—*Ostracotheres* H. Milne-Edwards (1853); *Dissodactylus* Smith, S. I. (1870); *Cryptophrys* Rathbun (1893), *Xanthista* White (1846); *Durckheimia* (Ruppel) de Man (1889); *Scleroplax* Rathbun (1893); *Raphonotus* Rathbun (1897); and *Pinnotheres* Latreille (1802). Under subfamily Pinnotherelinae Alcock, Tesch (1918) treated the genera *Pinnotherelia* H. Milne-Edwards and Lucas (1843); *Pseudopinnixa* Ortmann (1894); *Pinnixa* White (1846); and *Tetrias* Rathbun (1899). The subfamily Xenophthalminae Alcock is known from a single genus *Xenophthalmus* White (1846). The fourth subfamily Asthenognathinae Stimpson embraces the genera *Asthenognathus* Stimpson (1858); *Mortensenella* Rathbun (1909); *Tritodynamia* Ortmann (1894); *Hapalonotus* Rathbun (1897) [To replace *Malacosoma* de Man (1879) which is preoccupied]; *Opisthopus* Rathbun (1893); *Chasmocarcinops* Alcock (1900); *Voeltzkowia* Lenz (1905); and *Aphmodactylus* Tesch (1918).

In the course of the present study we have experienced the same difficulties as other recent workers who have dealt with members of the family Pinnotheridae, especially the genus *Pinnotheres* in that the taxonomy of this genus itself is in a nebulous state badly needing a critical review on a global basis.

As for the generic name *Pinnotheres*, Alcock (1900) felt that *Pinnoter* being the correct transliteration of the Greek word, which was also used by Rumph in 1705, 'no apology is necessary for reverting to it'. Tesch (1918) disagreeing with Alcock (1900) advocates using *Pinnotheres* drawing

attention to the ambiguity surrounding *Pinnotheres* in early Greek literature and sums up his argument with the statement that "Apart from such arguments it seems preferable not to cling too firmly to Aristotle or even Rumphus, but to return simply to authors using the regular Linnæan nomenclature and I see no reason to follow Alcock in his orthography."

The authorship of *Pinnotheres* ascribed to Latreille (1802-03) has been disputed and Direction 45 (1956) of the International Commission on Zoological Nomenclature was for the substitution of *Pinnotheres* Bosc (1801-02) for *Pinnotheres* Latreille (1802-03). (See also Monod Th. 1956.)

Neave's "Nomenclator Zoologicus" gives the following:

Pinnotheres (pro-theres Latreille, 1802) Leach, 1816.

Pinnothera (pro-res Latreille, 1802) Dana, 1851.

Pinnotheres Latreille (1802), *Hist. Crust. Ins.*, 3, 25-Crust.

Hardly any emphasis has been given up to now for the study of the species of *Pinnotheres* taking into account the possibility of polytypic species occurring in the genus; the host relationships and spatial distributional patterns of the species, etc., for a proper understanding of the species complexes in this genus. Difficulty in the taxonomy of this genus will be experienced by a reviewer as stable or dependable characters for distinguishing the species are not many and even so some of them have been proven to be affected during growth. In this connection, the need for taking into account the phenomenon of asymmetry in pea-crabs, when present, has been stressed by Gordon (1936). In view of these, the sanest course to follow in *Pinnotheres* taxonomy at present would be to refrain from describing new species on very ill-defined and variable characters, or merely on grounds of a new host record. These considerations have probably led some recent authors (Poisson, 1946; Barnard, 1950; Jones, 1950; Monod, Th., 1956; Dell, 1960) to describe or denote their finds as merely *Pinnotheres* sp., a course which we have also followed in the present study.

One of the notable works on *Pinnotheres* during the close of the 19th century is that by Burger (1895) who described as many as 30 new species from the Philippines and nearby islands. As already mentioned, Alcock's (1900) contribution has been towards a proper classification of the family Pinnotheridae itself, and in attempting this he has recorded 5 species of *Pinnotheres* from the Indian Seas. Other useful works dealing with Indian species of the genus *Pinnotheres* are those by Hornell and Southwell (1909), Southwell (1910), Chopra (1931), and Chhapgar (1957). The most important work to appear on Indo-Pacific Pinnotheridae is the provisional review of the group by Tesch (1918) wherein 57 species of the genus *Pinnotheres* are keyed and 65 species from the Indo-Pacific (excluding species from Eastern Pacific—the western coast of North and South America) are check-listed. Some criticism has been expressed by later workers on the usefulness of the key characters used by Tesch (1918) for separating the species of the genus *Pinnotheres*. This again draws attention to the urgent need for a taxonomic review of the genus based on a study of the type material and wherever possible additional series of specimens of the different species, preferably of both sexes.

Since 1918 when Tesch check-listed or referred to a total number of 76 species of the genus *Pinnotheres* from the Indo-Pacific (including Eastern Pacific), at least 21 new species have been described from this area up to 1963 and in addition about a dozen have been described or denoted merely as *Pinnotheres* sp. These do not include about 13 species reported at one time or other from the Atlantic and the Mediterranean. Before giving a list of these with host records and distributional details, we shall consider here two other aspects having a bearing on the taxonomy of the genus *Pinnotheres*, namely larval characters and their role in taxonomy and phylogeny, and asymmetry in *Pinnotheres*.

1. LARVAL CHARACTERS AND THEIR ROLE IN TAXONOMY AND PHYLOGENY

In this connection the remarks of Gurney (1939) appear pertinent. He has drawn attention to the fact that in spite of increase in our knowledge of decapod larvae in recent years, the larval

characters have not been used in the classification of the crabs. The considerable differences in the larvae of closely allied species of even a single genus and the difficulties of identification of the larvae if not linked with the adult are drawn attention to. As an example he cites the case of the differences between the species of *Pinnotheres* and allied genera with reference to telson and carapace and remarks that "... it is difficult to believe that the systematics of the adult can be correct. If typical zoeas of Pinnotherid, Eballiid, and Hymenostomatid crabs are taken they are found to have so many points of agreement that they must be supposed to be related; and yet each is now placed in a group widely separated from the others." His further observations on the larval and adult characters of certain species of *Pinnotheres* and allied genera such as *Dissodactylus*, *Pinnixa*, *Chaetopteryna*, *Ostracotheres* and *Tridacnae* have led him to conclude that the larval characters point to a relationship between Pinnotheridae, Leucosiidae, and Hymenosomidae and also suggest that the genus *Pinnotheres* may have to be subdivided. Since 1939 the larval stages of a few more species of *Pinnotheres* are known and for a natural classification within the genus as well as at the higher category levels it may also be necessary to take into account salient larval characters.

2. ASYMMETRY IN PEA-CRABS

De Man, one of the first to notice asymmetry in the length of the appendages of *Pinnotheres* at first considered this phenomenon as being due to the cross breeding between two species inhabiting the same molluscan host. However, in 1929 (p. 16) he considered this improbable. Gordon (1936) while discussing this phenomenon in greater detail has also enumerated some of the immediate problems in connection with this as: "(1) How many species of the large genus *Pinnotheres* are markedly asymmetrical; (2) whether it is characteristic of both sexes, or only the females; (3) whether or not the position of the female within the mollusc shell (should the asymmetry prove to be restricted to females of species inhabiting Mollusca) is constant and/such that growth of the legs on one side might be rather hampered, and (4) at what stage in the development of the Pinnotherids the asymmetry first becomes apparent." The taxonomist should give due consideration to these facts.

SPECIES OF THE GENUS *PINNOTHERES* LATREILLE

Pinnotheres abyssicola Alcock and Anderson (1899)

Distribution: Travancore coast (S.-W. Coast of India) from 430 fathoms.

Host: *Lima indica*.

References: Alcock and Anderson (1899), Alcock (1899, 1900), Hornell and Southwell (1909), and Tesch (1918).

Pinnotheres afinis Burger (1895)

Distribution: Ubay, Philippines; Gulf of Siam; Shantung (Coast of China).

Hosts: *Pinna* sp.; *Pecten hastatus* (?)

References: Burger (1895), Rathbun (1910), Tesch (1918) and Tu (1938).

Remarks: This species is different from *Ostracotheres affinis* H. Milne-Edwards (1853) described from Mauritius and later reported from the Red Sea by Nobili (1906). This clarification is necessary as some species of *Pinnotheres* have been placed under the genus *Ostracotheres* H. Milne-Edwards or vice versa by some workers.

Pinnotheres alcocki Rathbun (1910)

Distribution: Mergui Archipelago, Burma; Padang; Noordwachter Island near Batavia, Indonesia; Buriat, Philippines.

Host: *Cytherea* sp., *Mytilus* sp.

References: de Man (1881 a, 1888 b), Burger (1895), Alcock (1900), Rathbun (1910), Tesch (1918), Sakai (1935) and Gordon (1946).

Remarks: Rathbun (1910) proposed a new name for the material described as *Pinnotheres* (—*teres*) *parvulus* by de Man, Burger and Alcock (*nec P. parvulus* Stimpson, 1858).

***Pinnotheres angelicus* Lockington (1876)**

Distribution: Vera Cruz, Coast of California.

Host: ?

References: Lockington (1876), Miers (1880) and Tesch (1918).

***Pinnotheres arcophilus* Burger (1895)**

Distribution: Ubay, Philippines.

Host: *Arca* sp.

References: Burger (1895), and Tesch (1918).

***Pinnotheres ascidicola* Hesse (1871)**

Distribution: Coast of France.

Hosts: *Ascidia canina*, *Ascidia intestinalis*.

Reference: Hesse (1871).

***Pinnotheres barbatus* Burger (1895)**

Distribution: Aibukit, Philippines.

Host: *Donax* sp.

References: Burger (1895), and Tesch (1918).

***Pinnotheres bidentatus* Sakai (1939)**

Distribution: Wakayama Prefecture, Japan.

Host: Unknown.

Reference: Sakai (1939).

***Pinnotheres bipunctatum* Nicolet (1849)**

Distribution: Chile, W. Coast of S. America.

Host: ?

References: Nicolet (1849), and Tesch (1918).

***Pinnotheres boninensis* Stimpson (1858)**

Distribution: Bonin Island.

Host: "Small oysters."

References: Stimpson (1858, 1907), Tesch (1918), and Sakai (1935).

***Pinnotheres borradallei* Nobili (1906 a)**

Distribution: Red Sea; Minicoy Island, Laccadive Archipelago.

Hosts: *Mya* sp. (?); *Pinna* sp.

References: Borradaile (1903), Nobili (1906 a), Paulson (1875), and Tesch (1918).

Remarks: *P. borradallei* was proposed by Nobili (1906 a) for *P. tenuipes* Borradaile, 1903 (nec *P. tenuipes* Burger, 1895), and for *P. rouxi* Paulson, 1875 (nec *P. rouxi* H. Milne-Edwards, 1863).

***Pinnotheres burgeri* Rathbun (1920)**

Distribution: Gulf of Siam.

Host: Unknown.

References: Rathbun (1910), and Tesch (1918).

***Pinnotheres cardii* Burger (1895)**

Distribution: Buriyas, Philippines; Gulf of Siam; Japan.

Host: *Cardium unedo*.

References: Burger (1895), Rathbun (1910, 1924), Tesch (1918), and Sakai (1935).

***Pinnotheres coarcatus* Burger (1895)**

Distribution: Zamboanga, Philippines (brackish water).

Host: ?

References: Burger (1895), and Tesch (1918).

***Pinnotheres consors* Burger (1895)**

Distribution: Palos Island; Siboga Exped. Station No. 277 off Dammer Island, N.E. of Timor.

Hosts: *Clrce* sp.; *Arca* sp.

References: Burger (1895), and Tesch (1918).

Remarks: Tesch (1918) provisionally placed one female obtained at Siboga Exped. St. 277 under this species, at the same time drawing attention to the several characters in which the specimen differed from Burger's description of *P. consors*.

***Pinnotheres corbiculae* Sakai (1939)**

Distribution: Nagasaki; Kagoshima Prefecture, Japan.

Host: *Corbicula japonica*

Reference: Sakai (1939).

***Pinnotheres coutieri* Nobili (1905)**

Distribution: Red Sea.

Host: ?

References: Nobili (1905, 1906), and Tesch (1918).

Pinnotheres cyclinus Shen (1932)

Distribution: China Seas.

Host: *Corbicula japonica*.

Reference: Shen (1932).

Pinnotheres deccanensis Chopra (1931)

Distribution: Coast of Madras Presidency (S.E. Coast of India).

Host: *Holothuria scabra*.

Reference: Chopra (1931).

Remarks: Chopra (1931) has drawn attention to the affinities of this species to *P. ortmanni* Burger (1895) from Aibukit, Philippines.

Pinnotheres dilatatus Shen (1932)

Distribution: China Seas.

Host: ?

Reference: Shen (1932).

Pinnotheres dofteini Lenz (1914)

Distribution: Cape of Good Hope, Simons Bay, Algoa Bay, St. James, False Bay, Simons-town (Union of South Africa).

Hosts: Ascidians *Phallusia canaliculata* and *Pyura stolonifera*; also unidentified ascidians attached to ships; *Pinna* sp.

References: Lenz (1914), Tesch (1918), and Barnard (1950).

Pinnotheres edwardsi de Man (1888 b)

Distribution: King Island Bay, Mergui Archipelago, Burma; Siboga Exped. Stn. 258 off Tual, Kei Island; Siglap, Singapore; Abrolhos.

Hosts: *Ostrea* sp.; *Pinna* sp.

References: de Man (1888 b), Alcock (1900), Hornell and Southwell (1909), Tesch (1918), Montgomery (1931) and Gordon (1936).

Pinnotheres exiguus Burger (1895)

Distribution: Palapa and Samar Islands, Philippines.

Host: Unknown.

References: Burger (1895), Tesch (1918).

Pinnotheres flavus Nauck (1880)

Distribution: Zamboanga, Philippines.

Host: Holothurian.

References: Nauck (1880), de Man (1887), Burger (1895), and Tesch (1918).

***Pinnotheres glaber* Burger (1895)**

Distribution: Palaos Islands.

Host: *Tapes turgida*.

References: Burger (1895), and Tesch (1918).

***Pinnotheres glaberrimus* Burger (1895)**

Distribution: Zamboanga, Ubay, Philippines; Gulf of Siam (brackish water).

Hosts: *Arca* sp.; *Lama divaricata*.

References: Burger (1895), Rathbun (1910), and Tesch (1918).

***Pinnotheres globosus* Jacquinot and Lucas (1853)**

Distribution: Singapore; New Caledonia; Mozambique.

Host: ?

References: Jacquinot and Lucas (1853), H. Milne-Edwards (1853), Hilgendorf (1878), Tesch (1918) and Barnard (1950).

Remarks: After comparing the types of *P. globosus* Jacquinot and Lucas, and *P. obesus* Dana, H. Milne-Edwards (1853) considered the former to be a synonym of the latter. Tesch (1918: footnote on p. 257) did not agree with this treatment of *P. globosus*, but at the same time did not include this species in the list of species considered valid by him, nor as a synonym of any species.

Hornell and Southwell (1909) apparently following H. Milne-Edwards (1853) have considered *P. globosus* to be conspecific with *P. obesus* Dana. In their list of recorded species of *Pinnotheres* they have given *Meroe quadrata* and *Cytherea* sp., as hosts of *P. globosus* and mentioned "China Seas" as the distribution of this species. This is no doubt incorrect.

On the basis of Hilgendorf's (1878) record of this species from Mozambique, Barnard (1950) has listed *P. globosus* in his treatise on Decapod Crustacea of South Africa, and he has also mentioned this species in the key to the identification of South African species of *Pinnotheres* given by him.

***Pinnotheres gordonii* Shen (1932)**

Distribution: China Seas; Kisarazu Coast, Chiba Prefecture, Japan.

Hosts: Sugiura *et al.* (1960) record this species from: *Tapes japonica*, *Mytilus edulis*, *Ostrea* (*Crassostrea*) *gigas*, *Meretrix lusoria*, *Mactra veneriformis*, *Chlamys nipponensis* and *Umbonium* (*Suchium*) *moniliferum*.

References: Shen (1932), Sugiura, Kihara and Sugita (1960).

***Pinnotheres gracilis* Burger (1895)**

Distribution: Ubay, Philippines; Gulf of Siam.

Host: *Solen* sp.

References: Burger (1895), Rathbun (1910), and Tesch (1918).

Pinnotheres haiyangensis Shen (1932)

Distribution: China Seas.

Host: ?

Reference: Shen (1932).

Pinnotheres holothuriae Semper (1880)

Distribution: Zamboanga, Philippines.

Host: From cloaca of holothurian *Stichopus variegatus*.

References: Semper (1880), Burger (1895), and Tesch (1918).

Pinnotheres holothuriensis (Baker) (1908)

Distribution: St. Vincent Gulf, Edithburgh, South Australia.

Hosts: Holothurians and ascidians.

References: Baker (1908), Tesch (1918), and Hale (1927).

Remarks: This species was first described as *Ostracotheres* (?) ("*Pinnotheres*") *holothuriensis* by Baker (1908). Hale (1927) considers this a species of *Pinnotheres* and remarks that a variety of *P. holothuriensis* living in ascidians is very much smaller in size. We have provisionally placed this species under the genus *Pinnotheres* and additional comments are given under 'Remarks' for a similar problematic species *P. subglobosa* (Baker).

Pinnotheres impressus Burger (1895)

Distribution: Aibukit, Philippines.

Host: Unknown.

References: Burger (1895), and Tesch (1918).

Pinnotheres jamesi Rathbun (1923)

Distribution: Pichilique Bay, Lower California. (By electric light.)

Host: ?

Reference: Rathbun (1923).

Pinnotheres kamensis Rathbun (1910)

Distribution: Gulf of Siam.

Host: ?

References: Rathbun (1910), and Tesch (1918).

Pinnotheres kutensis Rathbun (1910)

Distribution: Gulf of Siam.

Host: ?

References: Rathbun (1910), and Tesch (1918).

***Pinnotheres lacquei* Sakai (1962)**

Distribution: Rocky bottom at Amadaiba, off coast of Hayama, Japan.

Host: From body cavity of brachiopod, *Laqueus rubellus*.

References: Sakai (1962).

***Pinnotheres laevis* Burger (1895)**

Distribution: Palaos Islands.

Host: *Coralliophaga* sp.

References: Burger (1895), and Tesch (1918).

***Pinnotheres lanensis* Rathbun (1910)**

Distribution: Gulf of Siam.

Host: ?

References: Rathbun (1910), and Tesch (1918).

***Pinnotheres latissimus* Burger (1895)**

Distribution: Manila, Philippines.

Host: *Paphia* sp.

References: Miers (1880), Burger (1895), Tesch (1918), Ohshima (1927), and Gordon (1936).

Remarks: Gordon (1936) considers *P. obesus* Miers (1880) (*nec* Dana, 1851) as a synonym of this species.

***Pinnotheres latus* Burger (1895)**

Distribution: Burias, Philippines; Palaos Island; Siboga Exped., Stn. 53, Nangamessi Bay, Sumba; Stn. 291, off Ambon.

Host: *Pinna* sp., *Pinna nigrina*.

References: Burger (1895) and Tesch (1918).

Remarks: Tesch (1918) draws attention to some differences between his Siboga Expedition material provisionally placed under this species, and Burger's account of *P. latus*.

***Pinnotheres lithodomi* Smith (1870)**

Distribution: Pearl Island, Coast of Panama, and vicinity.

Host: ?

References: Smith (1870), and Tesch (1918).

***Pinnotheres longipes* Burger (1895)**

Distribution: Aibukit, Philippines.

Host: Unknown.

References: Burger (1895), and Tesch (1918).

Pinnotheres lutescens Nobili (1905)

Distribution: Red Sea.

Host: ?

References: Nobili (1905, 1906 a), and Tesch (1918).

Pinnotheres mactricolus Alcock (1900)

Distribution: Mouth of Hooghly River, Bengal, India.

Host: *Mactra violacea*.

References: Alcock (1900, 1903), Hornell and Southwell (1909), and Tesch (1918).

Remarks: The species was originally described as *Pinnotheres mactricola* by Alcock (1900) who found it to show affinities to *P. cardii* Burger.

Pinnotheres maculatus Say (1818)

Distribution: From several localities from East Coast of North America.

Hosts: *Aequipecten irradians concentricus*; *Atrina rigida*; *Anomia simplex*; *Pinna* sp.; *Pecten magellanicus*; *P. gibbus*; *Modiolus modiolus*; *Mytilus edulis*; also known to occur in tubes of annelid *Chaetopterus variopedatus*.

References: Say (1818); Smith (1874, 1891), Sumner *et al.* (1913), Hay and Shore (1918), Fish (1926), MacGinite and MacGinite (1949), Christensen and McDermott (1958), McDermott (1961), and Sastry and Menzel (1962).

Pinnotheres maindroni Nobili (1905)

Distribution: Red Sea.

Host: ?

References: Nobili (1905, 1906 a), and Tesch (1918).

Pinnotheres major (Ortmann) (1894)

Distribution: Japan.

Host: ?

References: Ortmann (1894), and Tesch (1918).

Remarks: This species was originally described by Ortmann as *Pinnaxodes major*.

Pinnotheres malaguena Garth (1948)

Distribution: Malaga Bay, Columbia.

Host: Unknown.

Reference: Garth (1948).

Pinnotheres margarita Smith (1870 ?)

Distribution: Coast of California; Coast of Panama; and adjacent regions (W. Coast of S. America).

Host: ?

References: Smith (1870?), and Rathbun (1911).

Remarks: A redescription of the species was given by Smith in 1870.

Pinnotheres margaritiferae Laurie (1906)

Distribution: Kondatchi Paar, Pearl Banks off Ceylon, Gulf of Mannar.

Hosts: *Pinctada margaritifera*, *P. vulgaris*, *Mytilus* sp.

References: Laurie (1906), Hornell and Southwell (1909), Southwell (1910), and Tesch (1918).

Remarks: The species was originally described as *Pinnoteres margaritiferae*.

Pinnotheres marioni Gourret (1886)

Distribution: ?

Host: ?

References: Gourret (1886).

Pinnotheres modiolicolus Burger (1895)

Distribution: Philippines.

Host: *Modiola philippinarum*.

References: Burger (1895), and Tesch (1918).

Pinnotheres moseri Rathbun

Distribution: Jamaica, West Indies.

Host: *Ascidia nigra*.

References: Goodbody (1960).

Pinnotheres mytilorum (Herbst) (1782-1804)

Distribution: French Coast.

Host: ?

References: Herbst (1782-1804), and Lucas (1881).

Pinnotheres nigrans Rathbun (1910)

Distribution: Gulf of Siam.

Host: ?

References: Rathbun (1910), and Tesch (1918).

Pinnotheres novae-zealandiae Filhol (1886)

Distribution: Punipet, Auckland, and several other localities from New Zealand.

Host: ?

References: Filhol (1886), Heller (1865), Lenz (1901), Tesch (1918), Powell (1947), and Scott (1961).

Remarks: Scott (1961) has shown that records of *P. pisum* from New Zealand by Heller (1865) and others (nec *P. pisum* Pennant) refer to only variations of *P. novae-zealandiae*, which she con-

siders to be a polytypic species and the sole representative of the genus in New Zealand. Thus in all probability *P. schauinslandi* Lenz (1901) should also be a synonym of this species.

***Pinnotheres nudifrons* Burger (1895)**

Distribution: Lapinig, Philippines.

Host: Unknown.

References: Burger (1895), and Tesch (1918).

***Pinnotheres nudus* Holmes (1895)**

Distribution: Santa Cruz, Monterey Bay, Coast of California.

Host: ?

References: Holmes (1895, 1900), Weymouth (1910), and Tesch (1918).

***Pinnotheres obesus* Dana (1851)**

Distribution: Fiji Islands; Borneo; Gulf of Siam; Siboga Expedition Stn. 174 off Waru Bay, North Coast of Ceram.

Hosts: *Arca* sp.

References: Dana (1851, 1852), Rathbun (1910), Hornell and Southwell (1909), and Tesch (1918).

Remarks: Tesch (1918) considers *P. siamensis* Rathbun (1910) from Gulf of Siam as a synonym of this species. We have elsewhere drawn attention to the work of Hornell and Southwell (1909) (p. 1199) wherein these authors consider *P. globosus* Jacquinot and Lucas (1853) as a synonym of this species, which is not correct. Gordon (1936) has shown that *P. obesus* Miers (1880) (*nec* Dana, 1851) given as a synonym under this species by Tesch (1918) is in fact a synonym of *P. latissimus* Burger.

***Pinnotheres obscurus* Stimpson (1858)**

Distribution: Hong Kong.

Host: ?

References: Stimpson (1858, 1907), and Tesch (1918).

***Pinnotheres onychodactylus* Tesch (1918)**

Distribution: Siboga Expedition Stn. 172, between Gisser and Ceram Laut.

Host: ? (unknown).

Reference: Tesch (1918).

Remarks: Tesch (1918) remarks that this species shows close affinities to *P. rhombifer* Burger, *P. coarctatus* Burger, *P. tenuipes* Burger, and *P. borradallei* Nobili.

Pinnotheres orcutti

Distribution: W. Coast of North America.

Host: ?

Reference: Glassel (1938)

***Pinnotheres ortmanni* Burger (1895)**

Distribution: Aibukit, Philippines.

Host: Unknown.

References: Burger (1895), and Tesch (1918).

***Pinnotheres ostrearius* Rathbun (1918)**

Distribution: Delagoa Bay, St. James, and Cape Peninsula, Union of South Africa (Stebbing, 1920).

Hosts: From *Modiola* sp. shell and ascidian (Stebbing, 1920).

References: Rathbun (1918), and Stebbing (1920).

***Pinnotheres ostreum* Say (1817)**

Distribution: From several localities along the East Coast of North America.

Hosts: *Crassostrea virginica*, *Anomia simplex*, *Mytilus edulis*, *Pecten* sp.

References: Say (1817), De Kay (1844), Stimpson (1859), Rathbun (1884), Paulmier (1905), Hay and Shore (1918), Fish (1926), Christensen and McDermott (1958), McDermott (1961), and several other authors.

Remarks: This species is definitely known to be parasitic on the American oyster *Crassostrea virginica*, as reports by several workers (Strauber, 1955; Christensen and McDermott, 1958; and others) would indicate.

***Pinnotheres palaensis* Burger (1895)**

Distribution: Palaos Islands.

Hosts: *Arca scapha*, *Arca* sp., *Placuna sella*, *Byssarca* sp.

References: Burger (1895), and Tesch (1918).

***Pinnotheres parvulus* Stimpson (1858)**

Distribution: China Sea; Japan; Gulf of Siam.

Hosts: *Meroe quadrata*.

References: Stimpson (1858, 1907), Ortmann (1894), Rathbun (1910), Tesch (1918), Hornell and Southwell (1909), Makai (1931), and Sakai (1935).

Remarks: Reference may be made to our comments given under *P. alcocki* Rathbun.

***Pinnotheres pectinicolus* Burger (1895)**

Distribution: Fundordt, Ubay, Philippines; Red Sea.

Hosts: *Pecten radula*.

References: Burger (1895), Nobili (1906 a), and Tesch (1918).

***Pinnotheres pectenculi* Hesse (1871)**

Distribution: Coast of France.

Host: *Paetenculus flammelatus*.

Reference: Hesse (1871).

***Pinnotheres perezii* Nobili (1905)**

Distribution: Persian Gulf.

Host: ?

References: Nobili (1905, 1906 *b*), and Tesch (1958).

***Pinnotheres pernicolus* Burger (1895)**

Distribution: Ubay, Philippines; New Guinea; Red Sea.

Host: *Perna* sp.

References: Burger (1895), Nobili (1899, 1906 *a*), and Tesch (1918).

***Pinnotheres pholadis* de Haan (1835)**

Distribution: Japan.

Host: *Pholadis japonicae*.

References: de Haan (1835), Ortmann (1894), Adensamer (1897), Tesch (1918), and Sakai (1935).

Remarks: Tesch (1918), and Sakai (1935) consider *P. pisoides* Ortmann (1894) as a synonym of *P. pholadis* de Haan.

***Pinnotheres pichilinguei* Rathbun (1923)**

Distribution: Pichilingue Bay, Lower California. (By electric light.)

Host: ?

References: Rathbun (1923).

***Pinnotheres pinnotheres* (Linnaeus)**

Distribution: Coast of Camaron and Gabon, W. Africa; Puget Sound, Washington State, N.-W Coast of America.

Hosts: *Pinna* sp.; excurrent region of atrial cavity of tunicates (Wells, 1940).

References: Balss (1922 *b*), Wells (1940), Christensen and McDermott (1958) and other authors.

***Pinnotheres pilumnoides* Nobili (1905)**

Distribution: Red Sea.

Hosts: In sponges and holothurians.

References: Nobili (1905, 1906 *a*), Laurie (1915), and Tesch (1918).

***Pinnotheres pisoides* Ortmann (1894)**

Distribution: Japan.

Host: ?

References: Ortmann (1894), Tesch (1918), and Sakai (1935).

Remarks: Tesch (1918), and Sakai (1935) consider this species a synonym of *P. pholaides* de Haan.

***Pinnotheres pisum* (Pennant) (1777)**

Distribution: From several places along the coast of Europe (France, Belgium, Denmark, Sweden, etc.) and from the British coast (England, Wales).

Hosts: *Mytilus edulis*, *Cardium norvegicum*, *Spisula solida*, *S. elliptica*, *S. subtruncata*, *Modiolus modiolus*, and *Modiola modiolaria*.

References: Pennant (1777), Hesse (1871), Lucas (1881), Bouvier (1940), Gils (1947), Poulson (1949), Smith and Weldon (1958), Christensen (1959, 1962), Houghton (1963), and several others.

Remarks: The records of *P. pisum* from New Zealand waters have been shown to refer to *P. novae-zealandiae* by Scott (1961). Tesch (1918) gives the authorship of this species as: '*P. pisum* (Linné) Latreille'.

***Pinnotheres placunae* Hornell and Southwell (1909)**

Distribution: Balapur and Rann Bays, Beyt Island, all in the Gulf of Kutch, India; Tampalkam Bay near Trincomalee, Ceylon.

Host: *Placuna placenta*.

References: Hornell and Southwell (1909), Tesch (1918), and Chhappgar (1957).

***Pinnotheres politus* (Smith)**

Distribution: Chile.

Hosts: ?

References: Lenz (1902), Rathbun (1911), Tesch (1918), and Garth (1957).

Remarks: This species was originally described under the genus *Ostracotheres*. Tesch (1918) considers this as a species of *Ostracotheres* with the remarks that it resembles *O. cynthiae* Nobili by the last pair of the legs being longer than the preceding legs, but differing in the distinctly broader than long carapace, the more slender last pair of legs and the host being a lamellibranch instead of an ascidian. However, Garth (1957) considers this a species of the genus *Pinnotheres*.

***Pinnotheres pugettensis* Holmes (1900)**

Distribution: Coast of California; Puget Sound, Coast of Washington State, N.-W. Coast of U.S.A.

Hosts: From excurrent region of atrial cavity of tunicate *Cynthia* sp., and *Tethyum aurantum*.

References: Holmes (1900), Way (1917) and Tesch (1918).

***Pinnotheres purpureus* Alcock (1900)**

Distribution: Andaman Islands; Felidu Atoll, Maldive Archipelago; Red Sea.

Host: *Ostrea* sp.

References: Alcock (1900, 1903), Borradaile (1903), Nobili (1906), and Tesch (1918).

Remarks: This species is said to show affinities to *P. palaensis* Burger by Alcock (1900).

***Pinnotheres quadratus* Rathbun (1910)**

Distribution: Gulf of Siam; Siboga Expedition Stn. 34, Labuan Pandan, East coast of Lambok; Stn. 152, Wuncoch Bay, N.-W. Coast of Waigau Island.

Hosts: *Arca* sp.

References: Rathbun (1910), and Tesch (1918).

Remarks: Tesch (1918) has provisionally placed a male and a female pea-crab from the Siboga Expedition collections under this species and at the same time drawn attention to the differences between his specimens and the description of the species given by Rathbun.

***Pinnotheres rhombifer* Burger (1895)**

Distribution: Ubay, Philippines.

Host: *Pectenculus aurifluus*.

References: Burger (1895), and Tesch (1918).

Remarks: Tesch (1918) remarks that *P. rhombifer* Burger could be identical with *P. palaensis* Burger and that his species *P. onychodactylus* shows affinities to both these species.

***Pinnotheres ridgewayi* Southwell (1910)**

Distribution: Kondatchi Paar, Ceylon Pearl Banks, Gulf of Mannar; Kundugal Point, Pamban Island, Gulf of Mannar.

Hosts: *Pinna bullata*; *Pinna aequilatera*.

References: Southwell (1910), Tesch (1918), Gravely (1927), Prasad and Tampi (1959), and Sankarankutty (1965).

***Pinnotheres rotundatus* Burger (1895)**

Distribution: Burias, Philippines.

Host: *Circe* sp.

References: Burger (1895), and Tesch (1918).

***Pinnotheres rouxi* H. Milne-Edwards (1853)**

Distribution: Indian Ocean.

Hosts: ?

References: H. Milne-Edwards (1853), Tesch (1918).

Remarks: *P. rouxi* Paulson, 1875 (*nec* H. Milne-Edwards) has been considered as a synonym of *P. borradalei* Nobili.

***Pinnotheres rouxi* Rossignol (1957)**

Distribution: Pointe-Noire, French Congo.

Host: *Donax* spp.

References: Rossignol (1957, 1962).

Remarks: Rossignol (1957) has described the species as *Pinnoteres rouxi*. As the original description is not available to us for reference, we have provisionally placed this species separately. The specific name *P. rouxi* is preoccupied and if Rossignol's species is meant to represent a species different from *Pinnotheres rouxii* H. Milne-Edwards, then a new name will have to be proposed of this West African species.

***Pinnotheres sanguinolariae* Pillai (1951)**

Distribution: Ashtamudi Lake, Travancore Coast (S.-W. Coast of India).

Host: *Sanguinolaria diphos*.

Reference: Pillai (1951).

Remarks: This species is said to be allied to *P. gracillis* Burger. The generic name is given as *Pinnotherus* by Pillai (1951).

***Pinnotheres schauinslandi* Lenz (1901)**

Distribution: New Zealand.

Host: *Mytilus* sp.

References: Lenz (1901), and Tesch (1918).

Remarks: Scott (1961) considers all species of *Pinnotheres* recorded from New Zealand as being referable to a single polytypic species, *P. novae-zelandiae*.

***Pinnotheres semperi* Burger (1895)**

Distribution: Java, Indonesia.

Host: From Cloaca of *Holothuria fusco-cinerea*.

References: Burger (1895), Tesch (1918), and Gordon (1934).

***Pinnotheres serrignathus* Shen (1932)**

Distribution: China Sea.

Host: ?

Reference: Shen (1932).

***Pinnotheres setnai* Chopra (1931)**

Distribution: Viper Island and Dunda's Point, Port Blair, Andamans.

Host: From main respiratory system of an unidentified holothurian.

Reference: Chopra (1931).

Remarks: Chopra (1931) remarks that his species is closely allied to *P. semperi* Burger.

***Pinnotheres siamensis* Rathbun (1910)**

Distribution: Gulf of Siam.

Host: ?

References: Rathbun (1910), and Tesch (1918).

Remarks: Tesch (1918) considers this species a synonym of *P. obesus* Dana (1851).

***Pinnotheres silvestrii* Nobili (1901)**

Distribution: West coast of S. America.

Host: ?

References: Nobili (1901), and Tesch (1918).

***Pinnotheres similis* Burger (1895)**

Distribution: Ubay, Philippines.

Host: ?

References: Burger (1895), Tesch (1918), and Gordon (1936).

Remarks: Gordon (1936) has provisionally placed one ovigerous female collected from *Placuna placenta* at Siglap, Singapore, under this species "... until re-examination of the type for the nature of the walking legs."

***Pinnotheres sinensis* Shen (1932)**

Distribution: China Sea.

Host: ?

Reference: Shen (1932).

***Pinnotheres sinensis atrinae* Sakai (1939)**

Distribution: Kisarazu Coast, Chiba Prefecture, Japan.

Hosts: *Tapes japonica*, *Mytilus edulis*.

References: Sakai (1939), and Sugiura, Sugita and Kihara (1960).

Remarks: We have provisionally placed *P. sinensis* from Japan mentioned by Sugiura *et al.*, (1960) under this subspecies, as the forma typica (*P. sinensis* Shen) is known from the China Sea.

***Pinnotheres socius* Lanchester (1901)**

Distribution: Pulau Bidan, Penang, Malayasia.

Host: A Bivalve.

References: Lanchester (1901), and Tesch (1918).

***Pinnotheres spinidactylus* Gordon (1936)**

Distribution: Siglap, Singapore.

Host: *Modiolus philippinarium*.

Reference: Gordon (1936).

Remarks: This species is said to be closely related to *P. parvulus* Stimpson.

***Pinnotheres subglobosa* (Baker) (1908)**

Distribution: St. Vincent Gulf, South Australia.

Hosts: *Chlamys bifrons*, *Spondylus tenellus*, *Modiolaria australis*.

References: Baker (1908), Tesch (1918), and Hale (1927).

Remarks: This species was originally described by Baker (1908) as *Ostracotheres* (?) ("*Pinnotheres*") *subglobosus*. According to Tesch (1918) this species, as well as *P. holothuriensis* de-

scribed by Baker from South Australia do not belong to *Pinnotheres* as the dactylus of the external maxillipeds are absent in both. He remarks that "...as the propodus of these maxillipeds is much widened distally, especially in *P. holothuriensis*, there is perhaps a greater affinity to *Cryptophrys* than to *Ostracotheres*, though the distal margin of this propodus is not obliquely-truncate, but rounded, as in the latter genus." Hale (1927) considers this a species of *Pinnotheres*.

***Pinnotheres taylori* Rathbun**

Distribution: Puget Sound, Washington State, N.-W. Coast of U.S.A.

Host: From excurrent region of atrial cavity of tunicates.

***Pinnotheres tenuipes* Burger (1895)**

Distribution: Ubay, Philippines.

Hosts: Holothurians.

References: Burger (1895), and Tesch (1918).

Remarks: *P. tenuipes* Borradaile (1903) (*nec* Burger) was given a new name, *P. borradailei* by Nobili (1905).

***Pinnotheres tivelae* Gordon (1936)**

Distribution: Muscat, Arabia.

Host: *Tivela ponderosa*.

Reference: Gordon (1936).

***Pinnotheres trapeziformis* (Nauck) (1888)**

Distribution: ?; Mazatalan, West Coast of Mexico.

Hosts: *Holothuria maxima*, *H. inornata*.

References: Nauck (1888), Burger (1895), and Tesch (1918). Also see deMan (1887, p. 721).

Remarks: Originally described as *Holothuriophilus trapeziformis* Nauck.

***Pinnotheres trichopus* Tesch (1918)**

Distribution: Siboga Expedition Stn. 281, Great Kei Island.

Host: *Meleagrina* sp.

Reference: Tesch (1918).

Remarks: The description is based on a single male associated with young females of *P. villosulus* Guerin. According to Tesch, "I should certainly declare it to be the male of this species were it not for a few differences, which perhaps are not sexual." He also draws attention to the similarities in the shape of the carapace and the resemblance in the minute dactylus of the external maxillipeds, and the walking legs in the two species.

***Pinnotheres tsingtaoensis* Shen (1932)**

Distribution: China Sea.

Host: ?

Reference: Shen (1932).

Pinnotheres veterum Bosc.

Distribution: Coast of Europe and England.

Hosts: *Pinna squamosa*; also from branchial chambers of *Ascidia mentula*.

References: Bosc (1801-2), Heller (1865), and Atkins (1926 a).

Pinnotheres vicajii Chhapgar (1958)

Distribution: Bombay, India.

Host: *Paphia malabarica*.

References: Chhapgar (1957, 1958).

Remarks: The description of the new species appeared one year later (Chhapgar, 1958) than a brief diagnosis of it published by the same author in 1957.

Pinnotheres villosissimus Doflein (1904 a)

Distribution: Padang; also several localities from Andaman Islands.

Hosts: Holothurians *Muelleria lacanora*, *Actinopyga mauritiana*.

References: Doflein (1904 a), Tesch (1918), and Chopra (1931).

Pinnotheres villosulus M. Guerin (1830)

Distribution: Timor; Torres Straits; Zamboanga, Ubay, Philippines; Siboga Expedition Stn. 261, Elat, Great Kei Island.

Hosts: *Meleagrina* sp., *Pinna chemnitzii*, and *Meleagrina margaritifera*.

References: M. Guerin (1830, 1844), Miers (1886), Burger (1895), Tesch (1918), and Rathbun (1924).

Remarks: Tesch (1918) has assigned one juvenile female collected from Siboga Expedition Stn. 261 from *Meleagrina* sp., to this species. In a foot note (p. 251) he refers to the use of the specific name *P. villosulus* as follows: "This species is referred by H. Milne-Edwards and Burger under the name *villosus*. I could not consult Guerin's original description in Voy. "Coquille," t. 2, 1830, p. 13, but in his subsequent work (Iconogr. Regne An., Crust. p. 7, pl. 4, f. 4) the species is named *villosulus*, which term is used by Miers. "Since we have also not referred to the original description of the species, the spelling as given by Tesch (1918) is followed here. Hornell and Southwell (1909) have listed two species "*P. villosus* Guir." and "*P. villasulus* Guerin and Minivelle" which no doubt refer to one and the same species *P. villosulus* M. Guerin.

Pinnotheres winckworthi Gordon (1936)

Distribution: Penang, Malaysia.

Host: *Paphia gallus*.

Reference: Gordon (1936).

Pinnotheres sp. Doflein (1904 a)

Distribution: Algoa Bay, Union of South Africa.

Host: ?

Reference: Doflein (1904 a).

***Pinnotheres* sp. Szüts (1921)**

Distribution: Adriatic.

Host: Ascidian.

Reference: Szüts (1921).

***Pinnotheres* sp. Awati and Rai (1931)**

Distribution: Bombay, India.

Host: *Ostrea cucullata*.

Reference: Awati and Rai (1931).

***Pinnotheres* sp. Poisson (1946)**

Distribution: Madagascar.

Host: *Ostrea vitrefacta*.

Reference: Poisson (1946).

***Pinnotheres* sp. Jones (1950)**

Distribution: Trivandrum to Cape Comorin (S.-W. Coast of India) and beyond as far as Tinnevely Coast, Gulf of Mannar.

Host: Brown mussel *Mytilus* sp.

Reference: Jones (1950).

***Pinnotheres* sp. Barnard (1950)**

Distribution: Mossel Bay and Delagoa Bay.

Hosts: Pearl Oyster *Avicula*; *Modiola* sp.

Reference: Barnard (1950).

Remarks: This is based on Stebbing's 1920 specimens described under the names *P. pisum* (?) Stebbing 1920 (*nec* Linnaeus); and *P. ostrearius* in part (Stebbing, 1920—"the Delagca Bay specimen"). According to Barnard, the elongate dactyli of the 4th and 5th legs distinguish this from the European *P. pisum*.

***Pinnotheres* sp. A. Monod (1956)**

Distribution: West Africa.

Host: ?

Reference: Monod (1956).

***Pinnotheres* sp. B. Monod (1956)**

Distribution: West Africa.

Host: ?

Reference: Monod (1956).

Pinnotheres sp. C. Monod (1956)

Distribution: West Africa.

Host: ?

Reference: Monod (1956).

Pinnotheres sp. D. Monod (1956)

Distribution: Pointe-Noire, French Congo, West Africa (sub-littoral).

Hosts: ?

References: Monod (1956), and Rossignol (1962).

Remarks: Rossignol (1962) uses *Pinnoteres* sp. for this species.

Pinnotheres sp. Dell (1960)

Distribution: Petre Bay, Chatham Islands (43° 57' S: 176° 47' W).

Host: *Nemocardium pulchellum*.

Reference: Dell (1960).

Pinnotheres sp. Silas and Alagarswami (1965)

Distribution: Malpe, North of Mangalore, West Coast of India.

Host: *Meretrix casta*.

Reference: Description given in the present account.

IV. ANNOTATED BIBLIOGRAPHY ON THE GENUS *PINNOTHERES* LATREILLE

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- SUGIURA, Y., A. SUGITA AND M. KIHARA 1960. The ecology of Pinnotherid crabs as pests in culture of *Tapes japonicas*. I. *Pinnotheres sinensis* living in *Tapes japonica* and the influence of the crab on the weight of the host's flesh (in Japanese with English summary). *Bull. Japanese Soc. Sci. Fish.*, 26 (2): 89-94 (*Pinnotheres sinensis* parasitic on *Tapes japonicus*; female ovigers found from July to October; size of berried crab varied with period in season; female pea-crab also capable of living free from host for 4-5 months as rearing in aquarium showed).
- SUGIURA, Y., M. KIHARA AND A. SUGITA 1960. The ecology of Pinnotherid crabs pest in culture of *Tapes japonicus*. —II. *Pinnotheres gordonii* living in *Tapes japonica* and the influence of the crab on the weight of the hosts flesh. *Ibid.*, 26 (2): 565-569 (*Pinnotheres gordonii* parasitic on *Tapes japonicus*).
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- 1913 b. A biological survey of the waters of Woods Hole and vicinity. Section III. A catalogue of the Marine fauna. *Ibid.*, 31 (1911): 663-675. (674—*Pinnotheres ostreum* and *P. maculatus*).
- SZÜTS, A. 1921. Az Adria tizlabu rakjai (The crustacean Decapoda of the Adriatic). *Allatt. Kozlem. Budapest*, 18: (1921): 13-22 (p. 47—*Pinnotheres* in ascidian).
- TRESCHE, J. J. 1918. The Decapoda Brachyura of the Siboga Expedition II. Goneplacidae and Pinnotheridae. *Siboga Expedition*, 39 C1: 295 pp., 18 pls. (Two new species described and figured: *P. trichopus* n. sp., pp. 256-257, pl. 17, fig. 6; and *P. onychodactylus* n. sp., p. 259, pl. 17, fig. 5; Notes and figures of six other species—*P. villosus*; *P. obesus*; *P. edwardsi*; *P. latus*; *P. consors*; and *P. quadratus*; Key to Indo-Pacific species of *Pinnotheres*; checklist of known species from Indo-Pacific.)

- THOMPSON, J. V. 1835. Memoirs on the metamorphosis and natural history of the *Pinnotheres* or pea-crabs. *Entomol. Mag.*, 3: 85-90. (First zoea of *Pinnotheres pisum* illustrated).
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- THORPE, W. H. AND F. G. W. JONES 1937. Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. *Proc. Roy. Soc. London*, Ser. B, 124: 56-81.
- TU, T. J. 1938. Ueber einige in Polychaetenrohren und Muscheln gefundene Dekapoden an der Kuste von Schantung. *Zool. Anat. Leipzig*, 122: 177-186. (*Pinnotheres affinis* and other species of the genus commensal with *Pecten*, *Ostrea*, etc., on the North China Coast.)
- URITA, T. 1926. A checklist of Brachyura found in Kagosima Prefecture, Japan (p. 18—*Pinnotheres pholadis* listed).
- VERRILL, A. E. 1869. On the parasitic habits of Crustacea. *Amer. Nat.*, 3: 239-250 (*P. ostreum* as a parasite for shelter).
- VERRILL, A. E. AND S. I. SMITH 1874 (see Smith, S. I., 1874) (description of female; colour; distribution; host tunicate *Tethyum aurzntium*).
- WAY, E. Brachyura and Crab-like anomura of Friday Harbour, Washington. *Pub. P. S. Biol. Sta.*, 1: 349-352 (pp. 360-361: *P. pugettensis*, and *P. concharum*).
- WELLS, W. W. 1928. Pinnotheridae of the Puget Sound. *Publ. P. S. Biol. Sta.*, 6: 283-314 [pp. 285-86: Genus *Pinnotheres* Latreille described; *P. pugettensis* Holmes, synonyms, figures (figs. 1-3)].
- 1940. Ecological studies on the Pinnotherid crabs of Puget Sound. *Bull. Univ. Washington Publ. Oceanogr.*, 2: 19-50. (*Pinnotheres pugettensis*, *P. taylori* and *P. pinnotheres* from excurrent region of atrial cavity of tunicates and species of allied genus *Fabia subquadrata* in *Modiolus modiolus*.)
- WELSH, J. H. 1932. Temperature and light as factors influencing the rate of swimming of larvae of the mussel crab, *Pinnotheres maculatus* Say. *Biol. Bull.*, 63: 310-326. (Temperature and light were found to be important factors determining the rate of locomotion of larvae of *P. maculatus*. The velocity of progression was related to the light intensity according to the expression $\log V = K \log I - C$, this treatment yielding rectilinear graphs which facilitated comparing effects of temperature and intensity of illumination.)
- WEYMOUTH, 1910. True crabs of Monterey Bay. *Leland Stanford Jr. Univ. Publ.*, No. 4, 53-54. (Family Pinnotheridae and Key to six genera of the family found in Monterey Bay area; pp. 53-54—*Pinnotheres nudus* Holmes records one female '... probably from Monterey Bay'; specimen figured).
- WHITE, K. M. 1937. *L.M.B.C. Memoirs*, 31, *Mytilus*. The University Press of Liverpool, pp. 1-177.
- WILLIAMS, G. AND A. E. NEEDHAM 1938. On relative growth in *Pinnotheres pisum*. *Proc. Zool. Soc. London*, 108 A: 539-556 (Differential growth in *P. pisum*).
- WOLVEKAMP, H. P. AND T. H. WATERMAN 1960. Respiration. In *The Physiology of Crustacea*. Edited by T. H. Waterman, Ch. 2: 35-100 (Reduction of gills to 3 pairs in *Pinnotheres* an adaptive feature).
- WOODWARD, H. 1886. Commensals and parasites of *Meleagrina margaritifera*. *Proc. Zool. Soc., London*, p. 176 (Records an interesting case in which a male Pinnotherid crab is enclosed in a cyst of pearl).
- YOKOYA, Y. 1928. Report on the biological survey of Mutsu Bay, 10, Brachyura and crab-shaped Anomura. In *Sci. Repts. Tohoku Imp. Univ.*, Ser. 4, 3: 773- . [*Pinnotheres pholadis* de Haan, recorded (p. 773)].
- 1933. On the distribution of Decapod crustaceans inhabiting the continental shelf around Japan, chiefly based on materials collected by S.S. "Soyomaru", during the years 1923-30. *J. College Agric. Tokyo Imp. Univ.*, 12(1): 208 (p. 208—*Pinnotheres pholadis* de Haan).
- YOUNG, C. M. 1960. *Oysters*. Collins, St. James Place, London, 1-118.

DISCUSSION

- Dr. C. V. Kurian: Can you call the pea-crab a parasite?
- Dr. E. G. Silas: The definition of a parasite is still in an unsettled state and in the absence of a term which can fit in here precisely, we have thought it better to call this as a case of parasitisation due to the damages caused to the soft parts of the clam.
- Dr. N. Krishna Pillai: Quite a large number of groups of invertebrates harbour crustaceans such as Copepods. It requires a lot of study to say if a particular animal is a parasite or not. With the present study I would suggest that the pea-crab is termed as an 'associate' of the clam and leave it until a fuller study is made.

- Dr. N. Balakrishnan Nair: Can we not call this as a case of predation than parasitisation?
- Dr. E. G. Silas: The clear damages caused in this particular case and from the instances available in the literature recording even mortality of oysters make us feel that this is a case of parasitisation and we do not want to coin any new term for this association.
- Dr. B. Patel: In *Anadora granosa* and *A. rhombia* harbouring pea-crabs we have observed that the amount of haemoglobin present was lower than in the non-infested ones. From our observations we have found that the population of *A. granosa* from the east coast was heavily infested with pea-crabs whereas from the west coast only *A. rhombia* was found infested. Can you explain this?
- Dr. E. G. Silas: This is the same as the case where pea-crabs have not been found in the Mandapam region in the clams such as *Meretrix casta* while they have been collected from the Malpe clams. The occurrence, whether seasonal or not, and distribution of the species are not yet clearly understood.

ADDENDUM

For making the references up to date, the following papers dealing with *Pinnotheres* which have appeared latter than 1965 are given below:

- COSTLOW, J. D. JR. AND C. G. BOOKHOUT 1966. Larval stages of the crab, *Pinnotheres maculatus*, under laboratory conditions. *Chesapeake Science*, 7 (3): 157-163 (Larvae of *P. maculatus* obtained from crab commensal in scallop *Aequipecten irradians* reared successfully in laboratory from hatching to crab stage; five zoeal stages (1-5) and one megalopa stage described and figured; comparisons of larvae of *P. maculatus* with known larval stages of *P. pisum* and *P. veterum*).
- JONES, S. AND S. MAHADEVAN 1967. Notes on animal associations. 5. The pea-crab *Pinnotheres deccanensis* Chopra inside the respiratory tree of the sea cucumber, *Holothuria scabra* Jager. *J. Mar. Biol. Ass. India*, 7 (2): 377-380.
- SHANKARAKUTTY, C. 1966. On Decapoda Brachyura from the Gulf of Mannar and Palk Bay. *Proceedings of the Symposium on Crustacea*, Marine Biological Association of India, 1965, Part I: 341-362 (Records *P. deccanensis* Chopra from host *Holothuria scabra* from Gulf of Mannar, and *P. ridgewayi* from host *Pinna* sp. from Palk Bay and Gulf of Mannar).