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On some commensal decapod crustaceans from Singapore (Palaemonidae and Porcellanidae)

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(With 2 plates and 17 figures in the text)

A description is given of a new species of pontoniinid prawn commensal with bivalves of the genus *Placuna*. The species is close to members of the genus *Conchodytes* but differs in extreme flattening and consequent modifications which can be taken as adaptations to its peculiar environment. In behaviour and morphology it differs strikingly from the well known bivalve commensal *Anchistus custos* Forskål but is equally well adapted for its commensal life. The presence of filtratory mouthparts represents an unusual adaptation. Redescriptions and morphological comments are also given for two little known commensal porcelain crabs. In these also it is possible to explain many of the morphological peculiarities in functional terms.

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is really is
a beautiful beastie

Introduction

It has long been known that many tropical decapod crustaceans are commensal or symbiotic with other organisms but most of the available information is scanty and scattered through the taxonomic literature. Johnson (1963) gave a summary of such forms at Singapore but subsequent collecting has shown this to be very incomplete. The present paper is concerned with a few species of unusual interest belonging to the subfamily Pontoniinae of the family Palaemonidae (Caridea) and the family Porcellanidae (Anomura). Both groups contain free living species and many commensal forms (Bruce, 1965; Haig, 1960; Holthuis, 1952; Johnson, 1961, in press; Patton, 1966, in press). Species within each illustrate early stages of adaptation to life in close association with other organisms and the effects of such association on the morphology of the commensals.

Morphology and systematics**Pontoniinae*****Chernocaris* gen. n.**

Pontoniid prawns living in the mantle cavity of the bivalve *Placuna*. Closely related to the genus *Conchodytes* but with: the whole body very strongly depressed; the lower portion of the branchiostegal regions of the carapace and the pleura of the anterior abdominal segments reflexed against the ventral surface; telson in resting position carried strongly flexed forwards against the ventral surface of the abdomen, elongate, strongly tapered and with three pairs of dorsal spines; posterior margin of the telson with only two pairs of large spines of which the outer pair are very stout and a single pair of spine-like setae which may correspond with the middle spines of other pontoniinids; inflected portion of the carapace with a longitudinal keel in its anterior portion subparallel to and some distance from the true ventral margin.

The distal portion of the endopodite of the third maxilliped is more reduced than in *Conchodytes* and there are other minor differences. The generic status is discussed under the single species assigned here.

The generic name is given because the appearance of the single known species is strongly reminiscent of a pseudo-scorpion.

***Chernocaris placunae* gen. et sp. n.**

(Figs 1 to 12)

Holotype: Telok Paku, Singapore, 8 April 1965, in *Placuna sella* (Gmelin) taken at low water spring tide level by Yeo Seh Boo, one non-ovigerous female, length with flexed abdomen about 12 mm, post-ocular carapace length 6.0 mm.

Other material: Same locality, level, host and collector, 25 November 1965, one male allotype, overall length with flexed abdomen about 9 mm, post-ocular carapace length 5.1 mm.

The holotype has been deposited in the British Museum (Natural History) (registered number: 1967.1.4.1). The allotype is in the collection of this department.

Both specimens were obtained by Mr Yeo in the course of a study of the anatomy of *Placuna*. I am grateful to him for passing them to me for description.

Description. The body is remarkably flattened. In the holotype with post-ocular carapace length 6.0 mm the maximum width, across the carapace, is 5 mm, whilst the maximum depth is somewhat less than 2 mm. In conformity with this the ventral portions of the carapace and the anterior abdominal pleura are sharply inflected against the ventral surface, the line of folding forming a permanent structural feature.

The exoskeleton is smooth and shining but a few minute pits and shallow transverse grooves are visible on both carapace and abdomen under high magnification.

With the exception of those features associated with the extreme flattening the carapace closely resembles those of species of *Conchodytes*. The rostrum is rather short and broad; it extends beyond the anterolateral angles of the carapace by less than half its length and scarcely over-reaches the first segment of the antennular peduncle; its basal width is about 0.9 of its length. It is flattened basally but becomes rounded and convex distally. This

distal portion is strongly deflexed and the tip is blunt. The infra-orbital angle forms a small, blunt, rounded projection. The rounded anterolateral angles of the carapace are produced anteriorly well beyond this projection. They attain to about the middle of the cornea. There is a well defined longitudinal ridge on the inflected portion of the carapace which runs backwards from the anterior margin at some distance from the true ventral border (Fig. 3).

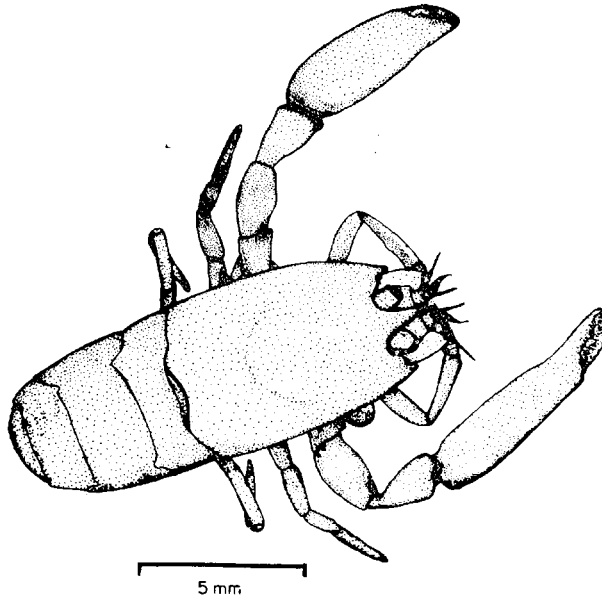


FIG. 1. *Chernocaris placunae* sp. n. Female holotype, dorsal view.

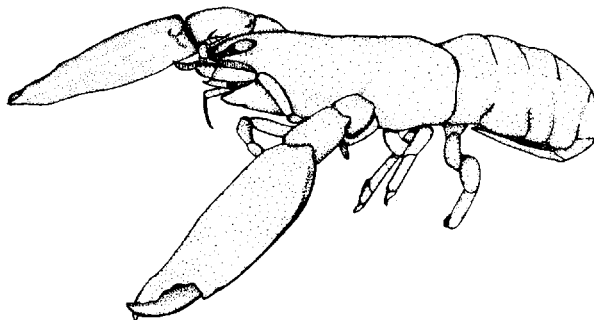


FIG. 2. *Chernocaris placunae* sp. n. Female holotype, oblique lateral view.

The abdominal segments are short and broad. Only the first three segments and part of segment four are visible in dorsal view. The fifth and sixth segments are turned forwards beneath the abdomen in "squat-lobster" fashion. The pleura of the first five segments are broadly rounded; those of the sixth are triangular with a rounded point. Those of the first three segments are well developed but those of the fourth are small and covered by

the pleura of the third when the abdomen is flexed. Those of the fifth and sixth segments are vestigial. The fifth segment is short and about 2.5 times as broad as long. The sixth segment is more elongate, about 1.5 times as long as the fifth and 1.3 times as broad as long. It is subrectangular with the posterolateral corners almost right angles and bluntly pointed.

The telson is nearly twice as long as the sixth segment and about as long as the uropods (Fig. 4). It is a little more than 0.4 times the post-ocular carapace length. At its widest the breadth is just over 0.5 times the length but it is strongly tapered so that the true posterior margin is somewhat less than 0.1 times the length. There are three pairs of rather large

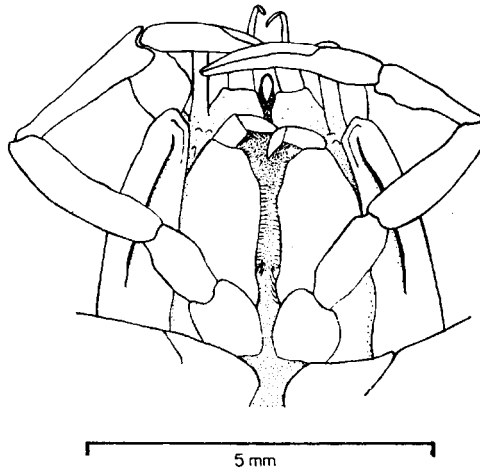


FIG. 3. *Chernocaris placunae* sp. n. Female holotype, ventral view of anterior portion.

dorsal spines at about 0.18, 0.68, and 0.90 of the length from the base. The telson is suddenly constricted beyond the most distal pair of spines. The short true posterior margin is strongly convex. It bears two pairs of large spines. The outer pair are very stout but at about midlength they are suddenly constricted to a narrow terminal portion. The inner pair are much more slender. Between the inner and outer spines there is a very slender setiform spine or spiniform seta. The posterior margin forms a bluntly rounded projection between the two inner spines. There are no setae between these two spines.

The first segment of the antennular peduncle is broad and flattened. It is strongly expanded laterally with the outer margin bending outwards in a convex curve distal to the stylocerite. The inner margin is almost straight. The stylocerite is short and broad and its tip is rounded and directed outwards. This first segment is more than 1.5 times as broad as long. Its outer angle is slightly produced as a rounded projection beyond the distal dorsal margin. The second segment is very short, more than twice as broad as long and only about one-third as long as the first segment. The third segment is slightly longer; together these two segments distinctly exceed half the length of the first segment. The distal margin of the second segment is oblique and the acute inner angle is produced forwards well beyond the outer angle. The outer margin is distinctly expanded laterally.

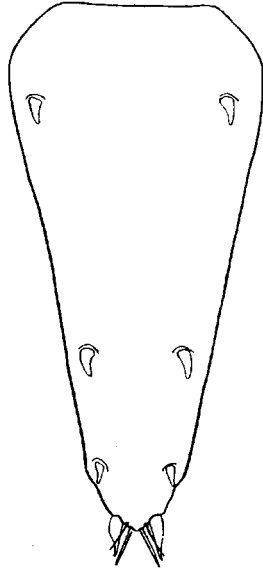


FIG. 4. *Chernocaris placunae* sp. n. Female holotype, telson, dorsal view.

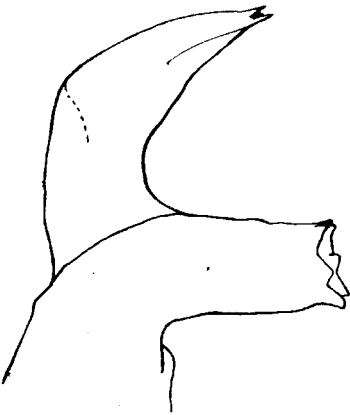


FIG. 5. *Chernocaris placunae* sp. n. Female holotype, mandible.

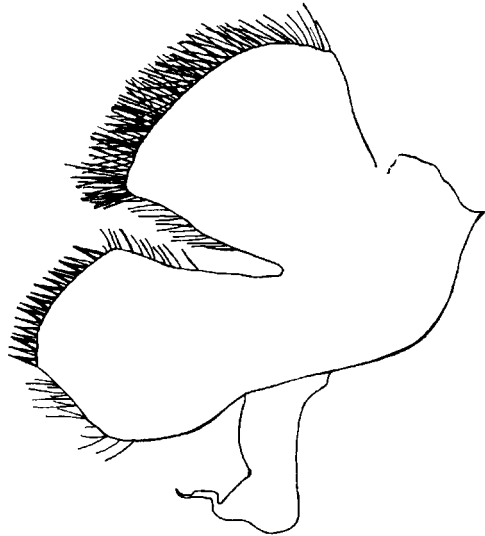


FIG. 6. *Chernocaris placunae* sp. n. Female holotype, first maxilla.

The flagella are short and stout. The ventral flagellum consists of ten annuli. The two rami of the dorsal flagellum are expanded and fused over most of their length, the fused region comprising 5.5 annuli. The longer ramus forms a slender projection of 4.5 annuli. The shorter appears to contain two complete annuli. It ends in a tuft of long setae reaching as

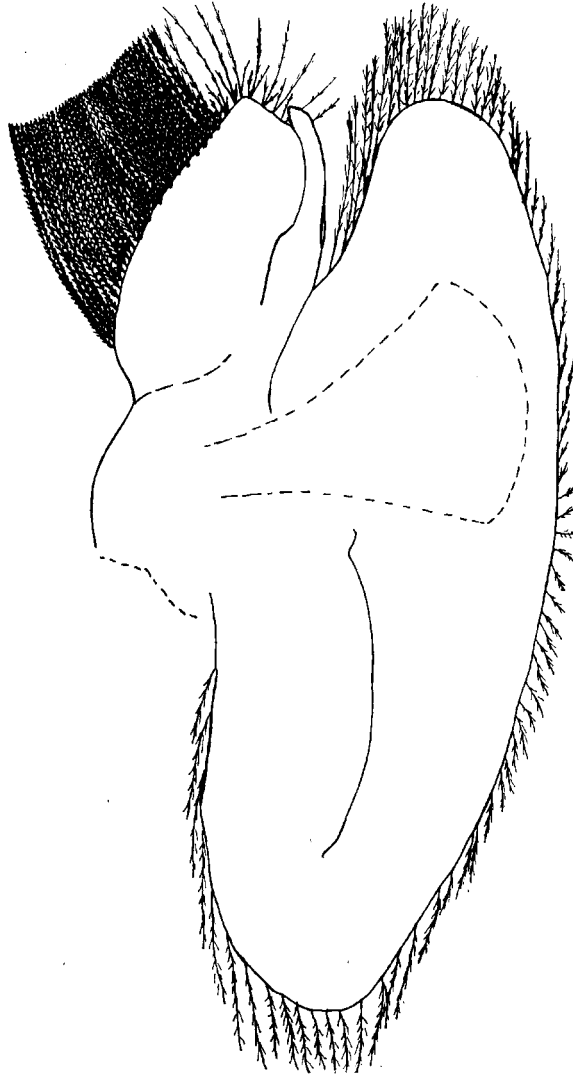


FIG. 7. *Chernocaris placunae* sp. n. Female holotype, second maxilla.

far as the end of the longer ramus. In their total structure these antennules closely resemble those of species of *Conchodytes*.

The lamina of the antennal scale slightly over-reaches the antennular peduncle. It is subelliptical with the setiferous inner margin somewhat more strongly convex than the outer margin. The distinctly incurved spine greatly over-reaches the lamina. The flagellum

is short. Its slender basal segment over-reaches the antennal scale. The distal portion contains ten annuli whose combined length is slightly greater than the basal segment.

The mouthparts closely resemble those of species of *Conchodytes* as described by Borradaile (1917) and Holthuis (1952). The small and rather weak mandibles lack any palp



FIG. 8. *Chernocaris placunae* sp. n. Female holotype, first maxillipede.

(Fig. 5). The distal portion is twisted so that the chisel-like end of the incisor process lies almost at right angles to the plane of the axis. As in *Conchodytes* this end is armed with a comb like row of five teeth of which the outer ones are the larger. The molar process is well developed and the circular grinding surface is provided with several blunt teeth.

The first maxillae closely resemble those of species of *Conchodytes* (Fig. 5). The proximal endite is armed with numerous very fine setiform spines arranged in several rows. The inner

margin of the distal endite is armed with two rows of shorter, stronger, and more widely spaced spines with a V-shaped groove separating the rows. The inner margin of the endite of the second maxilla is fringed with a row of very fine and regularly arranged filtratory setae (Fig. 7). Somewhat similar but less regularly arranged setae are borne on the distal margin and extend for a short distance on to the outer margin. This endite is strongly

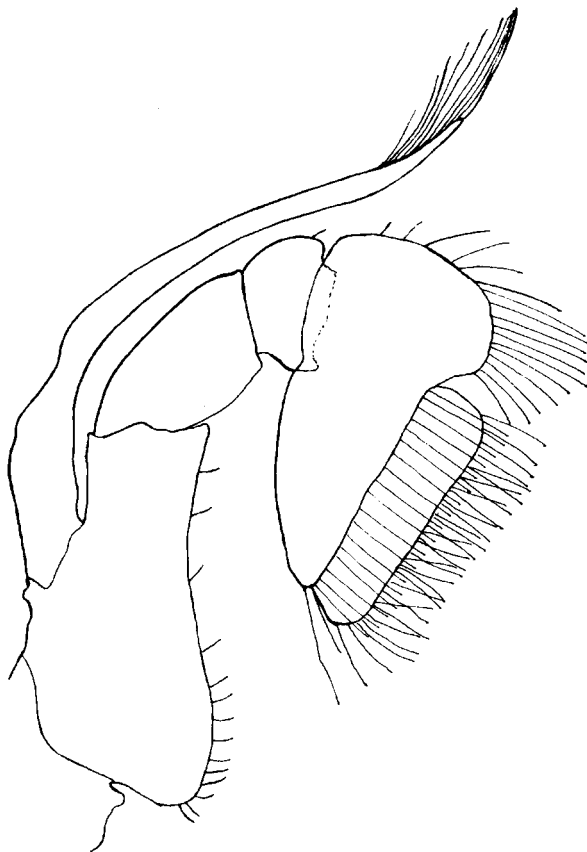


FIG. 9. *Chernocaris placunae* sp. n. Female holotype, second maxillipede.

curved in the transverse plane so that its anterior face is distinctly concave. The arrangement is a remarkably complete retention, or redevelopment, of the primitive filter-feeding type of endite and contrasts strongly with conditions in most commensal pontoninids. The endopodite is rather well developed; its broader basal portion is sharply set off from the narrow distal portion.

The first maxillipede (Fig. 8) is very strongly flexed along its longitudinal axis so that the posterior face is concave with the exopodite and epipodite lying almost at right angles to the endite. The epipodite has two strongly divergent lobes the anterior of which is smaller and partly overlapped by the exopodite. The exopodite has an expanded basal portion and a more slender distal prolongation of about the same length. Its outer proximal

corner is strongly bent backwards out of the plane of the rest of the segment. The short and rather broad endopodite is almost completely concealed in posterior view. The inner margin of the large endite is fringed with rather long, fine but stiff setae. Similar setae extend over most of the distal portion of the slightly concave anterior face. On the proximal



FIG. 10. *Chernocaris placunae* sp. n. Female holotype, third maxillipede.

portion of this face there is a single row of long and fine, closely set, filtratory setae with the concavity of the row facing anteriorly.

The second maxillipede (Fig. 9) closely resembles those of species of *Conchodytes*. The distal margin of the last segment is fringed with a complex arrangement of spines with outer and inner rows of slender spines, between which there are several rows of shorter,

coarser, and more closely set spines. The third maxillipedes also resemble those of *Conchodytes*. The well developed exopodite ends in a tuft of long, coarsely feathered setae. The two proximal segments of the endopodite are broadly expanded. The distal third of the inner margin of the proximal segment is fringed with very long, closely set, somewhat distally directed setae. The next segment is nearly 3.0 times as long as the proximal segment and 2.0 times as long as broad. Its inner margin is fringed with regularly arranged setae of almost uniform length which are distinctly shorter than those of the proximal segment. At the distal corner this row ends in a tuft of somewhat longer setae. There are a few setae on the inner portion of the distal margin and scattered setae on the outer margin. The palp has only two segments. It is set at a well marked angle to the rest of the limb. These segments together are only 0.6 times as long as the antepenultimate segment. The inner margins of both are provided with stiff setae. The ultimate segment also bears stiff setae on the distal portion of the outer margin and there are other setae scattered along the rest of this margin and that of the penultimate segment.

The extended first legs reach with the chela and most of the carpus beyond the antennal scale (Fig. 3). The whole limb is slender. The ischium is little longer than the basis and a little more than twice as long as broad. The merus is just over 1.8 times as long as the ischium and about 4.2 times as long as broad. It is somewhat compressed and slightly bowed. The elongate, conical carpus is equal to the merus and more than 4.5 times as long as broad. The chela is just over 0.8 times as long as the carpus and about 3.5 times as long as deep. The slender, tapering fingers are about 1.2 times as long as the palm. Their cutting edges are unarmed. The ventral border of the fixed finger bears numerous tufts of stiff bristles.

The second legs are massive in both sexes and in both sexes one is distinctly, though not greatly, stouter than the other and differs from it in structural details (Fig. 1). This stouter cheliped is the left in both specimens. In the female it is slightly shorter than the other cheliped. In the male these legs when fully extended over-reach the antennal scale by the chela, the carpus, and the extreme tip of the merus. In the female they over-reach this scale by the chela and carpus. In both they are a little more than twice as long as the post-orbital carapace length. These second legs are so carried that the chela lies almost in a horizontal plane but with the morphologically ventral border forming the internal border and at a slightly higher level than the morphologically dorsal border. The chela has thus been rotated from the primitive position by somewhat more than 90°. The following detailed descriptions are based on the holotype but the male does not show any important differences.

In the stouter leg the ischium is somewhat flattened and nearly 1.5 times as long as broad. The merus is stout and inflated with both anterior and posterior margins convex. It is about 1.5 times as long as the ischium and 2.0 times as long as broad. The carpus is about as long as the merus and broadly conical in shape. The distal border is somewhat oblique. It is about 1.5 times as long as broad. The chela, which is about 2.5 times as long as the merus, is about 2.5 times as long as deep. It is distinctly compressed and the ventral margin forms a definite though very blunt keel. The dorsal margin is broadly rounded. The strongly curved dactylus is a little less than 0.5 times as long as the palm. The fingers cross each other with the dactylus passing external to the fixed finger. Their cutting edges are armed with a few large teeth.

The more slender second leg differs mainly in the size and form of the chela. This is

about 3.0 times as long as the merus and about 3.0 times as long as deep. The ventral keel is somewhat better developed than in the stouter chela. The dactylus is distinctly less than 0.5 times as long as the palm. The fixed finger has two very conspicuous, large, blunt teeth. The dactylus has a broad, but low, blunt tooth in its proximal portion.

The third to fifth legs are rather slender. When fully extended the third leg reaches about to the end of the antennal scale. With the legs in normal walking position most of the long ischium is visible in dorsal view. It is little more than twice as long as broad and about 0.9 times as long as the propodus. The merus is slightly bowed and, like the more distal segments, it is definitely compressed. It is about 3.0 times as long as broad and 1.3 times as



FIG. 11. *Chernocaris placunae* sp. n. Female holotype, dactylus of third leg.

long as the propodus. The somewhat compressed carpus is elongate conical in shape. It is about 2.5 times as long as broad and 0.7 times as long as the propodus. The elongate rectangular propodus is about 4.0 times as long as broad. Each distal border is produced into a small acute tooth. The dactylus is only just over 0.2 times as long as the propodus. It is strongly compressed, short and deep (Fig. 11). Much of the length is occupied by the strong, curved, terminal claw, which is clearly delimited from the rest of the segment. The proximal portion is produced ventrally into a distinct hoof like projection which is not completely concealed when the dactylus is fully flexed. The junction of the ventral and distal margins of this projection forms a distinct angle which is produced into a very minute tooth in the male specimen. The ventral margin has a conspicuous fringe of stiff setae. Distal to this hoof like projection there is a strong, hook shaped, accessory claw which is, however, much smaller than the principal claw.

The uropods are about as long as the telson. The inner ramus is distinctly longer and narrower than the outer and both are rather narrowly elliptical. The setiferous portion of the margin of the outer ramus is separated from the true outer margin by a notch so minute that it is only perceptible under high magnification. There is a single minute uropodial spine which is only visible under high magnification (Fig. 12).

The male pleopods are of ordinary pontoniinid type.

Colouration. When preserved in alcohol the specimens are pale ivory with an almost imperceptible pink flush which fades away after a few months. In life the animal is very hyaline with a rosy flush. This flush is slightly deeper on the chelae and much deeper in a

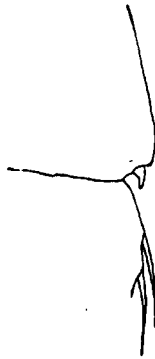


FIG. 12. *Chernocaris placunae* sp. n. Female holotype, part of outer margin of exopodite of uropod.

narrow band running along the lateral margins of the dorsal surface of the carapace and of the anterior abdominal segments. The proventriculus and hepatopancreas are visible by transparency and are greenish presumably because of contained food particles.

Behaviour. According to the collector the female lived for six weeks in the laboratory in association with its host. When removed from its host it returned there fairly rapidly.

I was able to make a few observations on the living animal removed from its host. Given a thin flat sheet of cardboard it preferentially settled on the flat surface, a behaviour which contrasts strongly with that of such pontoniinid commensals as *Anchistus custos* (Forskål) which settle on the edge of flat surfaces (Johnson & Liang, 1966). Walking was slow and clumsy and the animal did not increase its speed even when strongly stimulated. The initial response to attempts to dislodge it with a seeker was cessation of movement and firm anchoring by means of the dactyli of legs three to five. On continued stimulation it exhibited a slow backwards escape movement of an unusual nature. The hold was momentarily released and simultaneously the pleopods were flapped rapidly resulting in slow, clumsy, backward swimming. The tail-fan and general abdominal musculature did not appear to be involved in this movement. Slow, clumsy, forward swimming could sometimes be induced by stimulation from the rear but was not undertaken voluntarily.

No obvious feeding movements were noticed. The structure of the mouthparts indicates that the animal is a filter feeder. This is most unexpected since in other pontoniinids for which there is adequate information the mouthparts are such as to preclude filter feeding. It is possible that species of *Conchodytes* have filter feeding mouthparts but our knowledge

of these is still inadequate. The mechanism in *Chernocaris* differs in detail from the primitive malacostracan method and is to be regarded as an adaptation for commensalism enabling the animal to filter out food particles from the water streams in the mantle cavity of the host.

Systematic position. This species is clearly closely related to the genus *Conchodytes* which it resembles in major structural features. The most striking differences are the extreme flattening and the numerous minor modifications consequent on this. All can be regarded as adaptations for life in the very confined space offered by the mantle cavity of *Placuna*. Similar flattening, though not associated with pronounced structural modifications, is shown by the species of the crab *Pinnotheres* which also inhabit *Placuna*.

It would be feasible to treat this form as an aberrant species of *Conchodytes* were it not that it also shows several structural divergences which are not obviously connected with flattening. These include the orientation of the chisel edge of the incisor process of the mandibles and the form and spination of the telson. Taken together with the extreme flattening and associated modifications these differences seem to be sufficient to characterize a new genus *Chernocaris* of which *C. placunae* is the only species.

Porcellanidae

Polyonyx cometes Walker

(Plate I)

Polyonyx cometes Walker, 1887: 116-117, Plate 9, Figs 1 to 3; Johnson, 1958: 114-115; Johnson, in press.
Porcellana (Polyonyx) euphrosyne de Man, 1888: 221-224, Plate 15, Figs 1 to 3.

Material examined: 3 March 1966 off Changi Point, Singapore, in tube of large *Chaetopterus* on soft mud bottom, depth 6 m, collection R. U. Gooding, one ovigerous female c.b. 11.1 mm, one male c.b. 8.5 mm.

This species has so far only been known on the basis of the rather inadequate descriptions and old specimens of Walker and de Man. I had previously reported that the type was lost but the specimen (without type label but obviously the type)* has since been found in the collections of the British Museum (Natural History) (Johnson, in press). Since it is an old dry specimen it added little to our knowledge. The present specimens could be examined alive and freshly preserved to give considerable further information.

Structure. The carapace is transversely oval and only slightly convex dorsally. The shape of the front is as in Walker's description and de Man's figure and is thus intermediate between the shapes characteristic of the *obesulus* and *sinensis* groups. The grooves between the regions are well marked for this genus, especially anteriorly. The cardiac region is distinctly elevated with a steeply declivitous posterior face. At each side of this region there is a small and low, flat-topped, crescentic tubercle.

The animal is richly provided with long setae forming thick matted coats and fringes. A thick fringe of hairs runs along the dorsal border of the front concealing it in dorsal view and the same fringe extends along the lateral margins of the carapace. In the type specimen and in the male of the present collection these fringes extend inwards for some distance to form a setal coat over much of the branchial region. There is no such extension in the female specimen. With the exception of the extreme tips of the fingers the whole

* There is only one specimen, the holotype, in the British Museum (Nat. Hist.) collection. I. Gordon.

outer (upper) face of each cheliped from merus to dactylus is covered with a similar coat of long, matted setae. There are no setae on the inner face. The dorsal borders of legs two to four and of the ischium and merus of leg five are similarly fringed. There is a similar fringe on the ventral borders of legs two to four but this tends to be interrupted on the more distal segments of legs three and four. In the male the anterior two-thirds of the pterygostomial region are covered with a coat of somewhat shorter setae and there are small patches of such setae near the posterior and lateral margins of the dorsal surface of the abdominal segments. In the female this coat is restricted to the most anterior portion of the pterygostomial region and the abdominal patches are confined to the second segment.

The sternum, which is smooth and without setae, is broad and saddle-shaped and distinctly concave transversely.

The abdomen of the male is sub-rectangular and rather narrow. The telson has seven plates. Male pleopods are present.

The eyes and orbits are small. The antennules are of the usual type for the genus. The basal portion of the first antennal segment, surrounding the excretory pore, is hollowed out to accommodate the end of the peduncle and base of the flagellum of the first maxillipede. This region is bounded by an arcuate setiferous ridge. There are no other keels or spines.

The third maxillipedes are rather small and the food-collecting setae are rather fewer in number than in most porcellanids. The lamelliform internal expansions are large for the genus and that of the ischium is very large. The distal portion of the inner face of the carpus forms an excavation between dorsal and ventral lamelliform expansions. The proximal portion of the expansion of the propodus fits into this when the limb is flexed.

In both sexes one cheliped is larger and stouter than the other, the difference being most pronounced in the male. The large cheliped may either be the right or the left. In both chelipeds the fingers cross and do not gape.* In the large chela the dactylus passes external to the fixed finger; this arrangement is reversed in the small chela. At the base of the cutting edge of the dactylus of the large chela there is a moderately large tooth. In the male the remainder of this edge is entire except for an ill defined tooth, scarcely more than an angulation, at about the middle of its length. The fixed finger lacks any large teeth and is scarcely crenulate. In the female these edges resemble those of the male but are distinctly crenulate. The granulated ventral line on the chela mentioned by de Man is absent in both specimens. Apart from a few low ridges in the basal half of the upper surface of the merus the sculpturing of this cheliped is confined to exceedingly minute granules scattered rather uniformly over the upper surface and invisible unless the specimen is denuded. Possibly de Man misinterpreted these as fine punctuation.

In the small cheliped both fingers lack teeth and have the cutting edges crenulate in both sexes. The ventral granulated ridge is present but is obsolescent in the female specimen.

The dactyli of the walking legs have the distal claw much smaller than the ventral claw and only about 0.5 to 0.6 times as long. The distal claw is closely aligned with the dorsal margin of the ventral claw. Proximal to the ventral claw there is a single stout accessory tooth and proximal to that a slender median spinule. In the female specimen the spinulation of the ventral margins of the propodi is as described by de Man. In the male specimen

* Sankolli (1965) states that they gape but this statement appears to be based on a misinterpretation of de Man's figure.

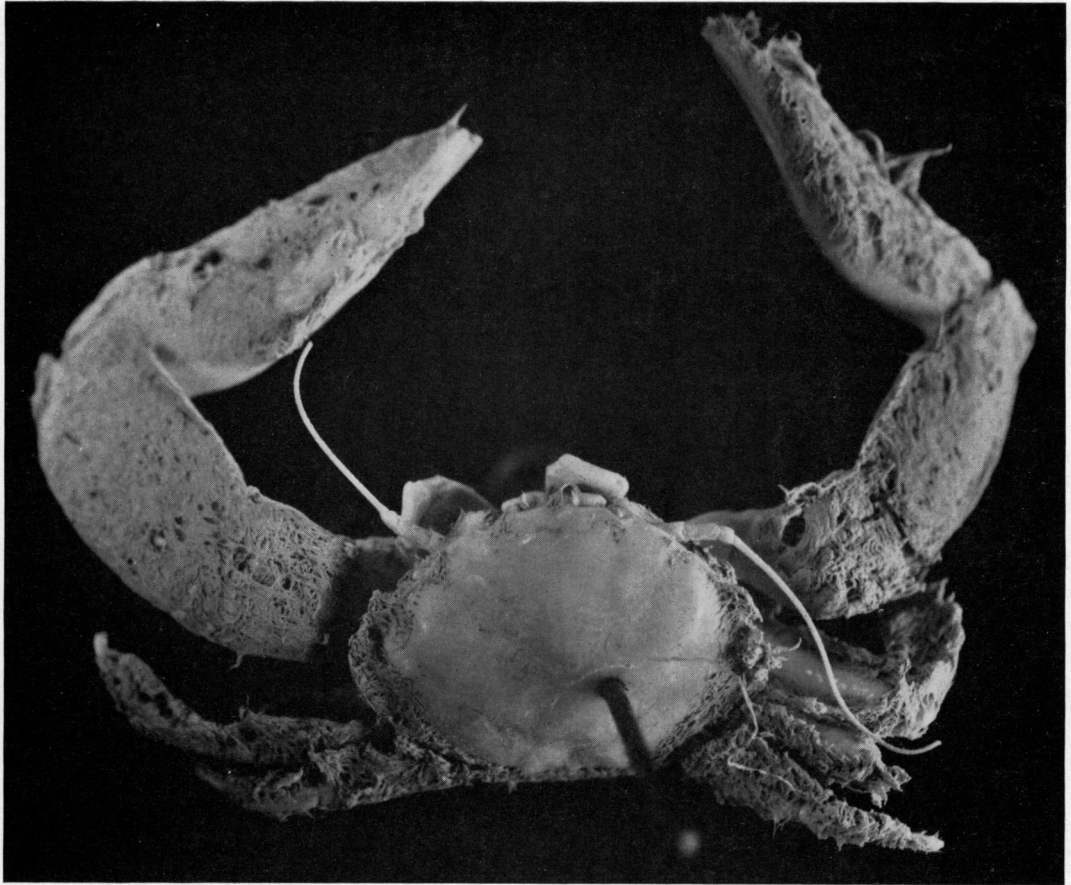


PLATE I. *Polyonyx cometes* Walker. Presumed holotype, dorsal view ($\times 6$).

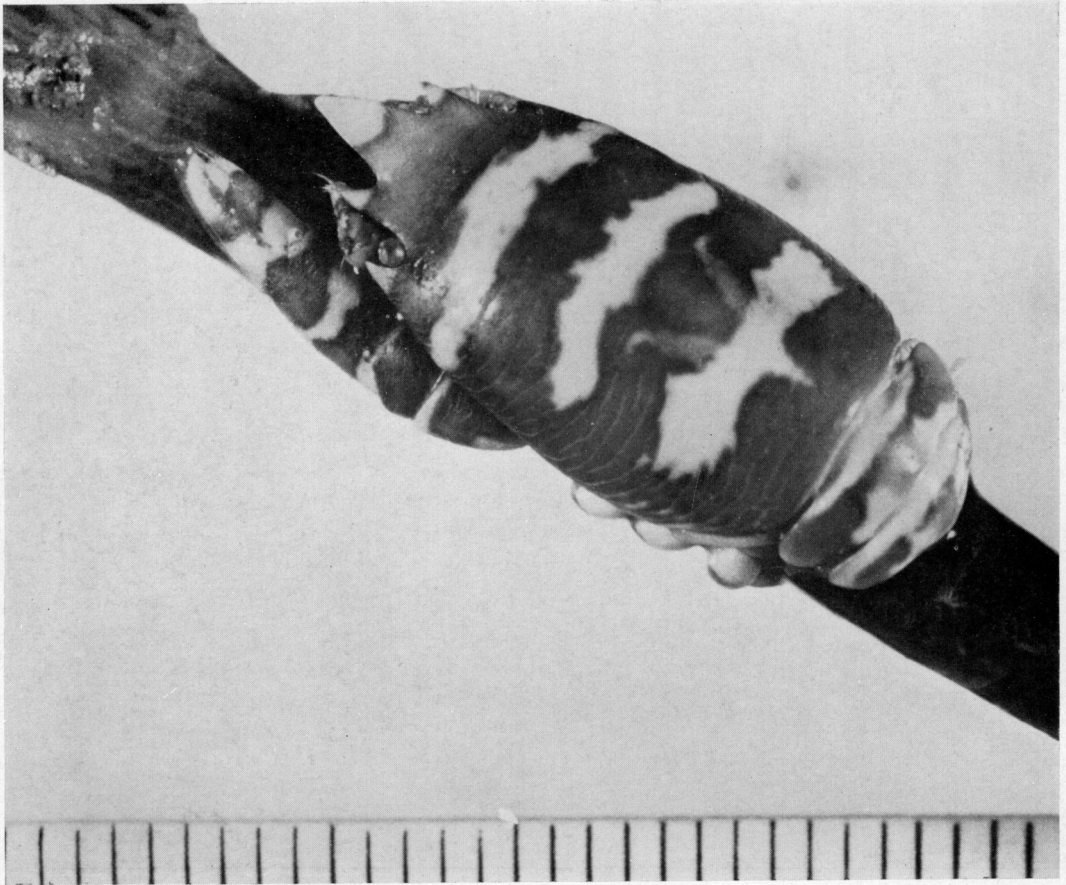


PLATE II. *Pseudoporcellanella manoliensis* Sankarankutty. Female, dorsal view in natural position on host (Scale in mm).

the spinules are somewhat stouter and I can only find the one in the middle of the length on the third leg.

Colouration. The ventral surface is almost pure white. In the male the dorsal surface is mid-testaceous, in the female pale testaceous. The groove in front of the cardiac region is paler in the male, white in the female. There are pale spots on the branchial regions and some less distinct mottling anteriorly. The intestinal region is white in both sexes. The tubercles at each side of the cardiac region are deep testaceous. The general setation is pale fawn and the setae of the antennules and maxillipedes are pale yellow. Noteworthy is the absence of the striking, species-specific arrangements of bright colours which are frequently found in free living porcellanids.

Habitat and behaviour. I had formerly supposed that this species must be commensal with *Aspergillum*. As Sankolli (1965) has pointed out this view derived from a misreading of de Man's statement which properly interpreted indicates a large annelid as host. The exact habitat remained unknown so that it is of interest that the species proves to be commensal with *Chaetopterus*, a genus with which several other species of *Polyonyx* are associated. The worm was a large one with the animal 16 cm long and the tube about 70 cm long and with a maximum diameter of about 2.5 cm. At the ends the tube was a little over 1 cm in diameter so that the crabs could presumably leave it if they attempted to.

The crabs were observed to make normal porcellanid feeding movements of the third maxillipedes. Presumably they feed by straining out small particles carried in the currents inside the tube of the host but unfortunately there are no data on the normal position of the crabs within the tube so that it is not clear whether they feed on particles in the food stream or on faecal matter.

When enclosed in a glass tube of similar diameter to that of the host tube the crabs settled with their transverse (longest) axis aligned along the axis of the tube. When the tube was closed so that the oxygen began to be depleted both began to make vigorous breathing movements of the pterygostomial regions of the carapace. Similar movements occur in a number of burrowing anomurans and the characteristic structure of the anomuran carapace, by allowing such movements, is an adaptation for life in confined spaces where oxygen may become depleted. Under these conditions the female also made fanning movements of the uropods and slow fanning movements of the egg-bearing pleopods. The male made no such movements.

Systematic position. Recently Sankolli (1965) described a new species of *Polyonyx*, *P. loimicola*, which he believes to be closely related to *P. cometes*. He tabulated the differences and resemblances between the two species using de Man's account of *P. cometes*. The present material allows for certain additions and corrections to be made to this comparison.

Size is the most striking difference between these two species, *P. loimicola* is much smaller, with ovigerous females not exceeding 8.5 mm in carapace width. This size difference conforms with the smaller size of the host and its tube.

The carapace of *P. loimicola* is transversely sub-rectangular rather than transversely oval and is strongly convex longitudinally. The distribution of dense setation is quite different in the two specimens as can be seen by comparison of Sankolli's figure with the plate of *P. cometes* given here. The carapace regions appear to be less well defined in *P. loimicola* and the cardiac region is broader and not flanked by tubercles. The shape of the sternum of the third maxillipedes is quite different in the two species. In *P. loimicola*

the central portion of the anterior margin is strongly convex whilst the anterolateral projections form curved horns. In *P. cometes* this central portion of the margin is broad and straight and the anterolateral projections are not horn like.

The fingers of the large cheliped gape in *P. loimicola* but not in *P. cometes*. The lamelli-form internal expansions of the third maxillipedes, especially of the ischium, are much larger in *P. cometes* than in *P. loimicola*. Sankolli notes as a difference between the species the presence of a spine in the middle of the ventral margin of the propodus of the walking legs in *P. cometes*. Since this character is inconstant, at least in the male, it cannot be used for discrimination.

Although *P. cometes* undoubtedly belongs to the *sinensis* group it is not closely related to any particular species within that group, not even to other species commensal with *Chaetopterus*. It has no close relationship with *P. sinensis* Stimpson. If the supposition of Stimpson (1907) and Shen (1936) that that species is commensal with *Chaetopterus* is correct it is surprising that the Singapore commensal should be such a distinct species.

Pseudoporcellanella manoliensis Sankarankutty

(Plate II, Figs 13 to 17)

Pseudoporcellanella manoliensis Sankarankutty, 1961: 92-95, Figs 1 to 8.

Material examined: 8 January 1966, off Changi Point, Singapore, clinging to stem of a sea-pen, *Scytalium* sp., seined by fishermen in about three fathoms, one male c.l. 16.9 mm, c.b. 8.6 mm, one ovigerous female, c.l. 16.4 mm, c.b. 9.1 mm.

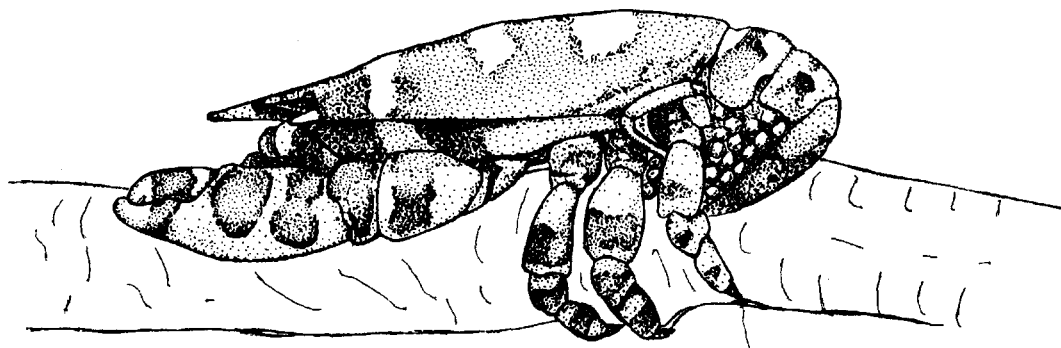


FIG. 13. *Pseudoporcellanella manoliensis* Sankarankutty. Ovigerous female, lateral view in life position on host.

Description. Sankarankutty's original description was based on a single immature specimen which it now appears was less than half grown. Consequently the description is in some respects incomplete and moreover contains some misinterpretations. The present, much more satisfactory, material allows of a fuller account.

The species is remarkable amongst Indo-West Pacific Porcellanidae because of its very elongate carapace and relatively well developed abdomen. In Sankarankutty's specimen and the present male the carapace is 1.96 times as long as broad. The female has a slightly broader carapace only 1.80 times as long as broad. The carapace is thus much more elongate even than that of the species of *Porcellana* (*Porcellanella*). The only other porcellanid

genus in which the elongation is at all comparable is *Euceramus* from the Atlantic and east Pacific, two of the three species of which are even more elongate. The abdomen is only partially concealed (a feature also found in *Euceramus*) and the whole build gives a strong, though superficial, resemblance to members of the family Chirostylidae, especially in lateral view (Fig. 13).

The animal is depressed but less so than most porcellanids and much less so than *Porcellana* (*Porcellanella*). Its carapace is convex transversely but almost flat longitudinally.

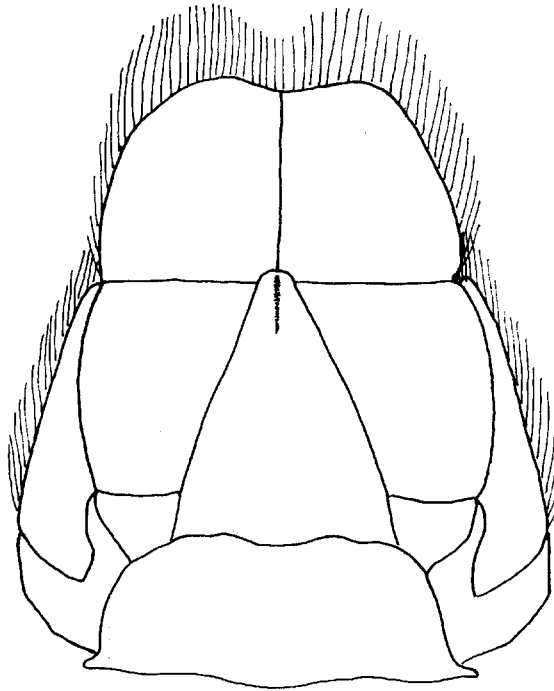


FIG. 14. *Pseudoporcellanella manoliensis* Sankarankutty. Telson, abdominal segment six and uropods.

The frontal region is produced into a flat, trilobed rostrum which is much more pronounced than that of *Porcellana* (*Porcellanella*). The ventral surface of the median lobe has a longitudinal keel which extends back between the bases of the antennules. The pterygostomial regions are very narrow. They are complete and consist of a single plate with strong oblique sculpturing. Each is produced anteriorly into a short, acute point separated from the dorsal plate of the carapace by a narrow but deep fissure (Fig. 16).

The narrow sternum is strongly concave in the transverse direction. It is polished, unsculptured, and hairless.

The second abdominal segment is rather broad and has relatively well developed, rounded pleura. The pleura of segments three to five are rudimentary and segment six lacks pleura. Segments four to six are narrow, especially in the male. The unusually elongate telson (Fig. 14) consists of seven plates. The uropods are rather small and in resting position are almost concealed by the telson. As in other porcellanids the under surface of the abdomen is membraneous.

The antennules (Fig. 15) are set side by side in shallow longitudinal pits on the ventral surface of the rostrum, separated medially by the rostral keel. The basal segment is produced externally into a lamelliform expansion which is not cut up into lobes or processes. It is fringed with long setae and bears scattered long setae on its ventral surface. In dorsal

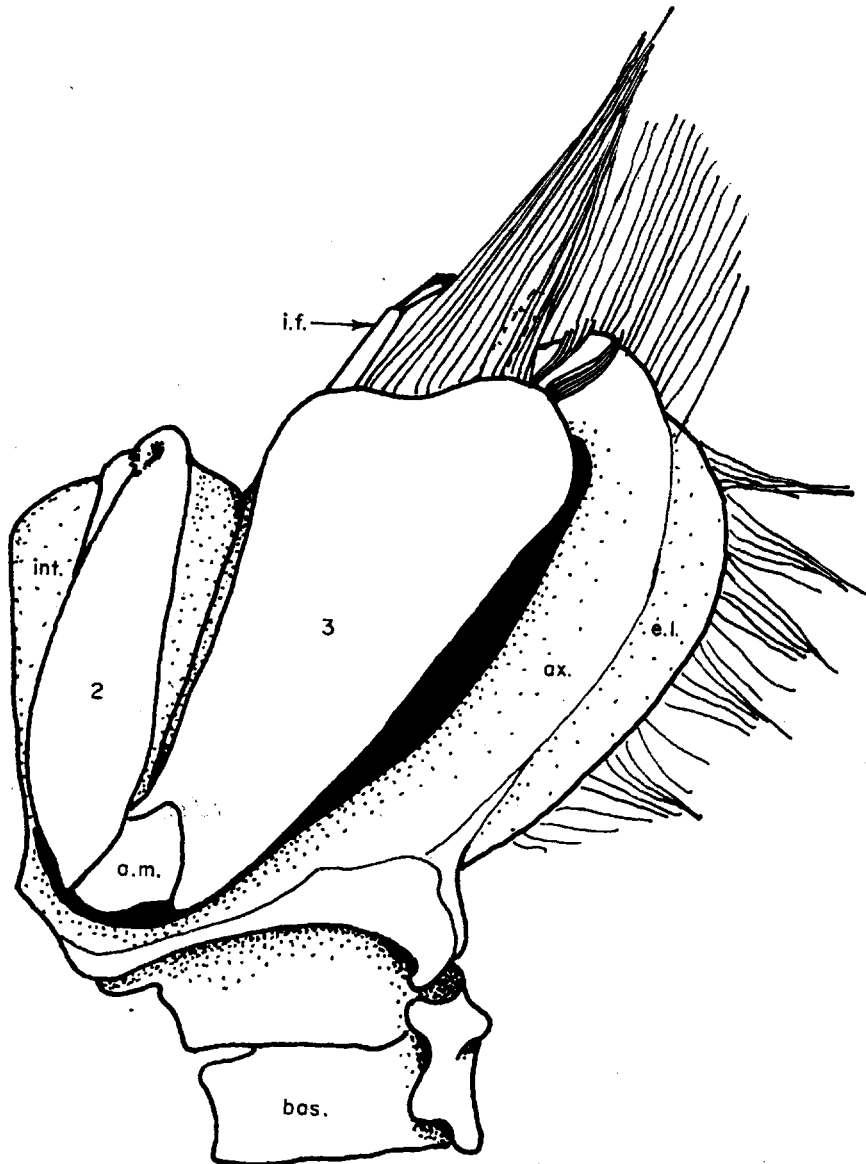


FIG. 15. *Pseudoporcellanella manoliensis* Sankarankutty. Right antennule, dorsal view.

a.m., Articular membrane; ax., axial portion of external expansion of basal segment; bas., basal portion of basal segment; e.l., external lamella of external expansion of basal segment; i.f., internal flagellum; int., internal portion of basal segment; 2, second segment; 3, third segment.

view this expansion is seen to consist of two sharply delimited portions, a thicker medial portion (ax.) and a thinner external lamella (e.l.). In normal orientation this expanded portion of the basal segment almost completely conceals the remainder of the appendage which can only be adequately seen when the appendage is removed and studied in dorsal view. In consequence the structure was seriously misinterpreted by Sankarankutty. The second segment (2) arises from the distal end of the medial portion of the basal segment and runs posteriorly along its dorsal face. The large third segment (3) runs obliquely in an antero-external direction dorsal to the lamelliform expansion of the basal segment and almost attains to the end of this expansion. It is flattened and expanded distally. Its distal border bears the usual setal fringe which is very long and dense. In dorsal view this fringe

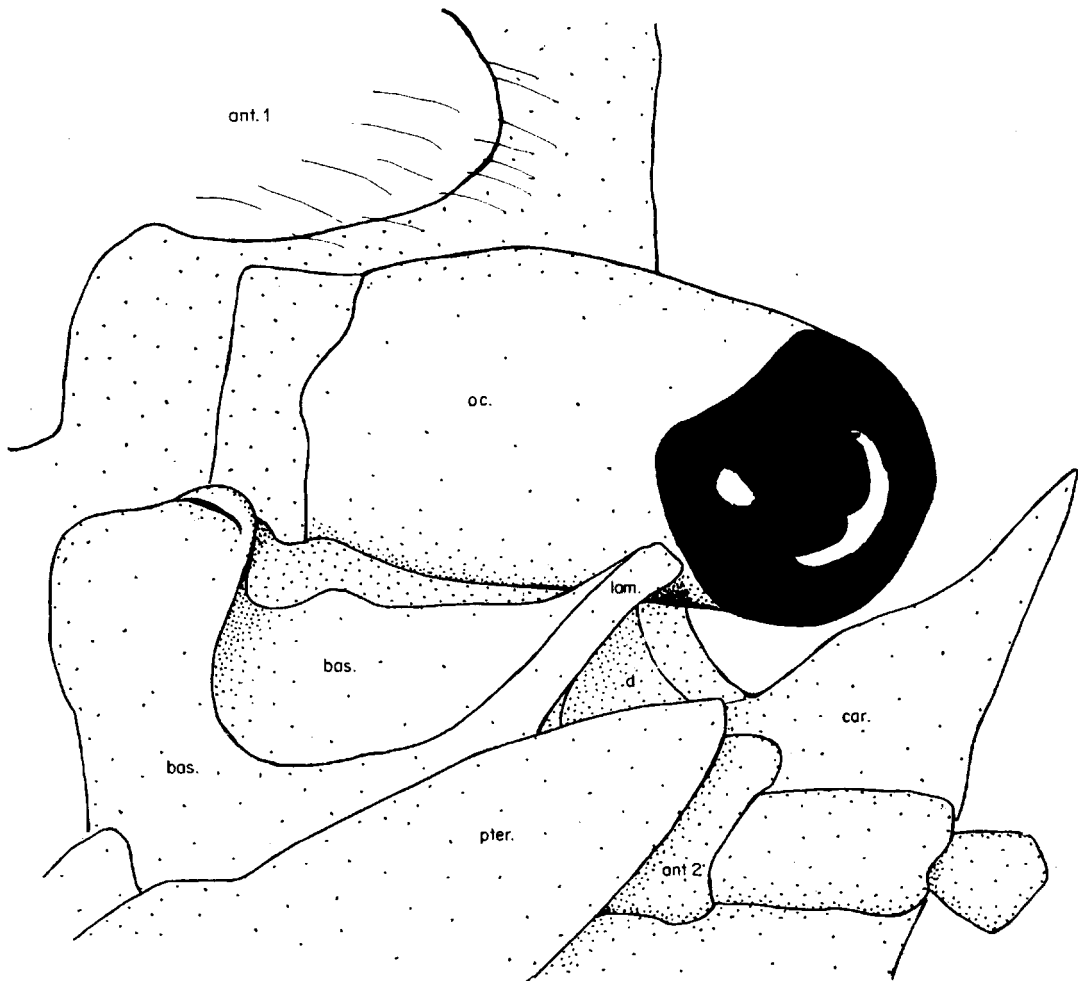


FIG. 16. *Pseudoporcellanella manoliensis* Sankarankutty. Slightly oblique ventral view of left orbital region. ant. 1, Basal segment of antennule; ant. 2, second segment of antenna; bas., basal segment of antenna; car., dorsal plate of carapace; d., dorsal projection of basal segment of antenna; lam., lamellar expansion of basal segment of antenna; oc., ocular peduncle; pter., pterygostomial region of carapace.

conceals the external flagellum and partially conceals the internal flagellum. Both flagella are very short, the external being slightly longer than the internal. This external flagellum is very slender and its structure is difficult to determine but it appears to contain ten annuli. The somewhat stouter internal flagellum (i.f.) possesses four annuli of which the most proximal is the largest.

The eyestalks (Fig. 16, oc.) lie laterally to the antennules and just medially to the antennae. They are short and broad. The cornea is rather small.

The antennae (Fig. 16, bas. and ant. 2) are very small and their structure is very difficult to determine so that they also have been misinterpreted by Sankarankutty. The basic structure appears to be close to and could be derived from that found in *Porcellana* (*Porcellanella*) but the proportions of the parts are very different. The basal segment (bas.) is elongate and rather narrow. Arising slightly posteriorly and laterally to the eyestalk it runs outwards and forwards parallel to the posterior border of that structure. Over most of its length it is covered ventrally by the exopodite of the second maxillipede (removed in the figure). It does not extend beneath the eyestalk anteriorly so that the orbit is very incomplete ventrally. For much of its length this basal segment is firmly in contact with and ankylosed to the anterior border of the pterygostomial region (pter.). Distally it is produced into a lamelliform expansion (lam.) which has a rounded distal border but which appears spine like in lateral view. This is evidently the "similar spiny projection anterior to the antenna" of Sankarankutty's description. The dorsal face of this basal process is produced (d.) to form a narrow but firm contact with the dorsal shield of the carapace (car.). This contact lies deep within the post-orbital fissure so that it is not easily observed and cannot be readily figured. The second segment (first free segment, ant. 2) is inserted on the dorsal face of the basal segment posterior to its articulation with the carapace so that this segment and the flagellum are excluded from the orbit. The remainder of this appendage is very short and the flagellum only contains six segments.

The large third maxillipedes (Fig. 17) extend forward beyond the mouthfield so as to cover the antennules. At rest the distal segments are strongly retroflexed to form a crab-like palp rather than carried partially extended as is usual in this family. The fringes of long setae proper to the family are still present and well developed but are almost completely concealed in ventral view. Most of the short exopodite is concealed by the endopodite. The basal portion of its peduncle has the ventral surface produced laterally into a triangular lamella. The flagellum is short and its base is strongly bent into an S-shaped curve.

The second maxillipedes are of ordinary porcellanid type. The endopodites are rather short and in resting position they are greatly over-reached by the peduncle of the exopodite. The flagellum is distinctly longer than that of the third maxillipede.

The remarkable short and massive chelipeds (Plate II, Fig. 13) are carried directed almost straight forwards and with the palm held in a near vertical plane. This orientation contrasts strongly with that found in most porcellanids where the chelipeds are carried with the palm in a near horizontal plane and the whole limb strongly flexed so that the chela is directed medially. The general structure of the chelipeds is adequately described by Sankarankutty. The ischium bears a blunt tubercle on its internal ventral margin. The merus is only elongated externally. Its internal border is short and is almost entirely occupied by a long, blunt, low tubercle. In these adult specimens the dorsal and ventral setal fringes described by Sankarankutty are confined to the fixed finger and the distal

portion of the dactylus. That on the fixed finger is subventral rather than truly ventral. There is a similar setal fringe on this finger parallel to and just ventral to the cutting edge. The inner faces of the fingers are somewhat excavated but lack setal fringes. The tips of the fingers cross, the dactylus passing internal to the fixed finger. In both specimens the

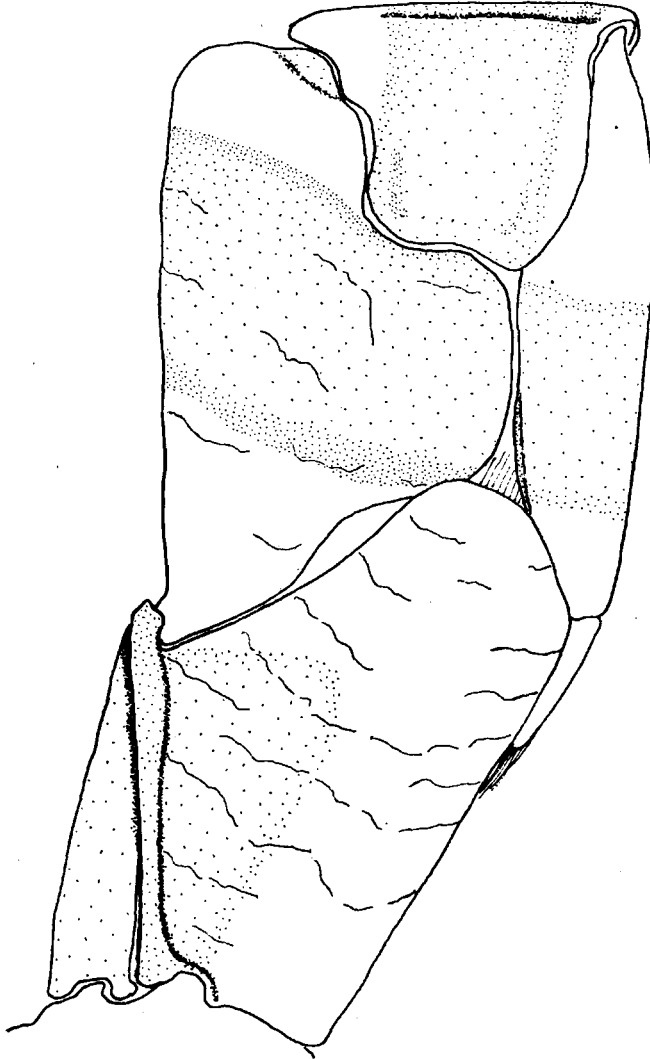


FIG. 17. *Pseudoporcellanella manoliensis* Sankarankutty. Right third maxillipede ventral view in resting position.

right chela is slightly longer and much more massive than the left. The teeth on the cutting edges of the fingers are larger and less regular on this chela. Both chelae have a slight gape which is more pronounced in the larger chela.

The short and stout walking legs are adequately described by Sankarankutty. In the adult they are of just the right length for clinging on to the stem of *Scytalium* (Fig. 13). It is impossible to remove living specimens without damage.

The fifth legs are of the usual porcellanid type; they arise close together and their bases are separated by a deep pit with a semicircular anterior margin. The ischium is about two-thirds as long as the merus and the carpus and merus are subequal. The propodus and dactylus are unusually setose.

The abdomen of the male specimen bears a single reduced pleopod which appears to arise from the left side of the fifth segment! Such an arrangement corresponds with nothing known elsewhere in the family and is presumably teratological. There are no other pleopods in the male.

Colouration. As is usual in this family the male is darker and more strikingly patterned than the female. The pattern is very bold (Plate II) and the colour does not match the red of the host. In the male the darker bands vary from slaty grey to almost black but in the female they are deep fawn. In both the pale bands are ivory. In preserved specimens the dark bands are a light reddish brown. The colouration fades rather rapidly but the pattern is still clearly visible after several months in alcohol.

This disruptive colouration serves as effective camouflage, at least to the human eye. Combined with the peculiar pose of the animal the effect is such that the animal appears to be an isopod like creature with the abdomen being interpreted as the head.

Systematic position. Sankarankutty, whilst pointing out that the only other porcellanid with such reduced antennae is *Minyoceras*, draws attention to resemblances to *Porcellana* (*Porcellanella*) and concludes that the systematic position is doubtful. He appears to believe that the form of the chelipeds and antennae show an approach to that in true crabs. These resemblances are superficial and the basic structure of the appendages is porcellanid.

In general form, form of front, and structure of the legs *Pseudoporcellanella* resembles *Porcellana* (*Porcellanella*) the members of which are likewise commensal with Pennatulacea. The antennules could be derived from the pattern found in that subgenus by comparatively small changes in orientation and folding. The antennae differ mainly in the lengthening and narrowing of the basal segment and the further reduction of the flagellum which is already somewhat reduced in *P. (Porcellanella)*.

The small and deep post-orbital fissure of *Pseudoporcellanella* corresponding to the longer and shallower groove of most porcellanids seems to be the result of reduction consequent on the reduction of the antennae.

The third maxillipedes could be derived from those found in *P. (Porcellanella)* by some reduction of the flagellum of the exopodite and comparatively small changes in the proportions and orientation of the segments of the endopodite. The telson, though more elongate, also closely resembles that of species of *P. (Porcellanella)*.

Some of the more striking differences are related to the differing modes of life of the two forms. The species of *P. (Porcellanella)* live amongst the broadly expanded "leaves" of *Pteroeides*, a habitat which is very different from the exposed position occupied by *Pseudoporcellanella*. Such differences include the greater elongation and convexity of the carapace in *Pseudoporcellanella*, the expanded second abdominal segment, the narrow and concave sternum, and the close set bases of the fifth legs. Other differences are less easily explained but are nonetheless probably adaptive modifications in *Pseudoporcellanella*. Such are the peculiar structure of the antennules and the extreme reduction of the antennal flagellum.

The apparent absence of male pleopods in *Pseudoporcellanella* is less important than at

first appears since these pleopods are often lost in this family. In the genus *Polyonyx* they are absent in *P. biunguiculatus* (Dana) but present in *P. obesulus* Miers (Haig, 1964) even though these two species are so similar that they have often been confused.

Thus, whilst generic distinction is certainly valid, *Pseudoporcellanella* is closely related to and derived from the *Porcellana* (*Porcellanella*) stock.

On the other hand the resemblances to *Minyoceras*, an obligate commensal of *Luidia* and ophiuroids (Haig, 1960), are probably convergent though both genera derive from the general *Porcellana* stock. Special resemblances are confined to a few features of chelipeds and antennae and the two genera differ markedly in other features.

Discussion

The three species considered here illustrate a number of problems of more general taxonomic interest which are best treated separately.

Apparent rarity of commensals

Although there are outstanding exceptions, such as the pontoninid *Anchistus custos*, most tropical Decapoda which are known or suspected commensals of organisms other than corals are represented by few specimens in museums and are generally considered to be rare; those considered here are no exception and none of them is known by more than five specimens.

Such rarity is probably only apparent. The mode of life is such that they are unlikely to be found during general crustacean collecting. They are only to be expected when the hosts are carefully examined for possible commensals. Even though they are quite common the hosts of these species are not ordinarily collected in large numbers since they are of little economic or aesthetic value and are not used for educational purposes. The fact that the commensals have been found at all in the limited available material indicates that they are probably common.

The history of the crab *Rhabdonotus pictus* A. Milne Edwards demonstrates that apparently rare commensals may nonetheless be abundant. Originally described in 1878, only one further specimen was reported until 1962 (Serène & Romimohtarto, 1963) although another, undoubtedly of the same species, was reported by Walker (1887) under the name *Caphyra archeri*. In the collections of several European museums I have only been able to find one further specimen (from Ceylon, identified as *C. archeri*, in the British Museum (Nat. Hist.) yet the species is abundant in the Johore Shoals area of Singapore. These and similar observations cast considerable doubt on the value of many general statements as to rarity or abundance which are based on general museum collections. Reliable assessments can only be made on the basis of extensive field work appropriate to the problem concerned.

Function and taxonomy

Cain (1959, 1964) has recently stressed the importance of what may be termed functional taxonomy. Within the Arthropoda the importance of such studies for higher levels of taxonomy has been well exemplified by the studies of Manton (summarized in Manton,

1958a,b, 1959; Tiegs & Manton, 1958). It is the author's view that such functional studies will prove of equal importance at the lower levels of crustacean taxonomy.

Unfortunately most tropical decapod crustaceans are only known from orthodox systematic accounts prepared on the basis of dead museum specimens; where biological observations have been made this has often been by workers such as Potts (1915) with no special interest in crustacean taxonomy as such. Sometimes indeed such data have been published without full identification of the organisms concerned so that they have been ignored by subsequent workers, as seems to have occurred for the sea-anemone commensal *Petrolisthes ohshimai* Miyake (Gordon, 1960).

Even where a taxonomist has worked on locally obtained commensals biological information may be quite inadequate and restricted to the name of the known or presumed host. Again accidents of division of work or exigencies of publication have resulted in the biological data being published separately from the taxonomic account, as has occurred for the species *Porcellana* (*Porcellanella*) *picta* (Stimpson) (Jones, 1959; Sankarankutty, 1961a,b) and *Polyonyx loimicola* (Sankolli, 1965; Sankolli & Shenoy, 1965).

There are thus considerable difficulties in the way of developing a functional taxonomy of these commensals. Nonetheless such an attempt appears to be worthwhile and the rest of this paper will be devoted to consideration of the functional taxonomy of the species dealt with in the present paper and in Johnson & Liang (1966).

Pontoniinid commensals of bivalves

The Indo-West Pacific prawns commensal with bivalves appear to fall into two groups centering around the genera *Anchistus* and *Conchodytes* respectively. We have some data on the functional morphology of *Anchistus custos* in the first group (Johnson & Liang, 1966) and of *Chernocaris placunae*, described above, in the second. Certain features are common to both, are found in other commensal prawns, and are generally accepted as adaptations to a commensal mode of life which could arise independently. Such are: the relatively clumsy form; the relatively weak abdomen; the reduced eyes and rostrum; and the short dactyli of the walking legs which end in strongly hooked claws.

The greatly enlarged second legs found in both species present a somewhat different problem. Similar enlargement is found in many other commensal pontoniinids including some, such as *Periclimenes brevicarpalis* Schenkel, which have almost certainly been independently derived from the primitive free living stock. One is thus tempted to regard this enlargement as a further example of a generalized and widespread adaptation to a commensal life. Against this view it is not easy to see how such enlarged chelae could be more advantageous to commensal than to free living prawns and it has not so far been possible to demonstrate any special functional significance for the enlargement. During the short observations of a living specimen of *Chernocaris* it made no use of these enlarged legs and did not even use them when it was "attacked" by a seeker. Johnson & Liang (1966) were similarly unable to demonstrate any aggressive, defensive, or sexual use in *Anchistus custos*, though they point out that behaviour of the male might be modified in the presence of receptive females. It is possible to consider these enlarged legs as heritage characters. It is well known that in the related subfamily Palaemoninae the second legs are often much enlarged, especially in the larger species and in large males (Holthuis, 1950). Thus one can envisage a basic genotypic pattern within members of this family which will tend towards the production of enlarged second legs unless modified by counter-selection.

The problem then becomes not, "Why do the commensals have enlarged second legs?" but, "Why are these legs much less enlarged in free living pontoniinids?" A partial answer may lie in the small size and relatively feeble build of most of the free living species. In such forms massive second legs would be a serious hindrance to active locomotion. In the commensal species the possibility of efficient, active locomotion is less important so that selection against enlargement of the second legs will be correspondingly relaxed.

The differences between these two species are as striking as their resemblances. *Chernocaris placunae* is much flattened and shows other modifications which stem directly from this flattening; *Anchistus custos* has a relatively high and little flattened body. In *C. placunae* the mouthparts are considerably modified for filter feeding; the third maxillipedes are operculiform (a convergence towards the higher Reptantia), and the first legs are of ordinary pontoniinid type; in *A. custos* the mouthparts are of more normal pontoniinid nature and are not filtratory, the third maxillipedes are not operculiform, and the first legs are peculiarly modified. These differences build up into two contrasting functional complexes associated with two distinct modes of life. *C. placunae*, living in the very confined mantle cavity of *Placuna*, sits on the flat surface of the gill lamella or mantle and obtains its food by filtering off particles brought into the mantle cavity by the feeding currents of its host. The flattening and type of mouthparts are both adaptations for this mode of life. Both would be highly detrimental if this prawn lived, as does *Anchistus custos*, clinging to the free edge of the gill lamellae and obtaining its food by using the first legs as scrapers.

Though numerous small differences remain unexplained the functional analysis explains most of the major differences between the two species. How are these findings to be interpreted taxonomically? In the absence of any functional analysis it would be reasonable to assume that the two species were only rather remotely related. The *Anchistus* and *Conchodytes* lines would represent separate invasions of the bivalve commensal niche. The functional analysis does not rule out this possibility since we can no longer accept the view that adaptive characters are of no value in classification or in tracing phylogeny (Cain, 1959). Nonetheless the analysis raises the possibility that these forms *may* be closely related. It is conceivable that all these Indo-West Pacific bivalve commensals are descended from a common stock of more generalized forms which first took to life in the mantle cavities of bivalves and thereafter split into diverging lines differing primarily in their method of food collection. On this view commensalism with bivalves becomes a character of greater taxonomic importance than many of the more obvious morphological characters of these forms.

Porcellanid commensals

Unless it is allowed that numerous lines have independently become commensals it is impossible to arrive at a rational classification of this family. The problem arises as to why commensal tendencies are so strong in this group. Free living species tend to be crevice dwellers and could thus become pre-adapted for a commensal life. Thus some features found in commensal species of *Polyonyx*, for instance the multi-unguiculate dactyli of legs two to four, are of obvious advantage to commensals but are found equally in free living species (Johnson, 1958).

Commensal tendencies are common in other crevice dwelling groups of decapods such as the alpheid prawns and the xanthid crabs. Nonetheless commensalism appears to be

altogether more frequent in the Porcellanidae. It is also frequent in such closely allied families as the Chirostylidae and Galatheidae.

There are other structural and biological features which pre-adapt porcellanids to a commensal way of life. Such is the characteristic food collecting mechanism in which the long setae of the third-maxillipedes are used to strain off particles from the water in a manner reminiscent of barnacles.

The carapace structure which allows for special respiratory movements may also be of value especially for tubicolous commensals. It may be that this mechanism functions best in a tube like space, though this could only be established after a full hydrodynamical analysis. Sankolli & Shenoy (1965) showed that individuals of *P. loimicola* removed from the host would die rapidly unless provided with tubes in which to live which suggests some such advantage though alternative explanations are possible.

The retention of well developed uropods by porcellanids is at first sight puzzling. The abdomen and its musculature are much too reduced for these appendages to have any important locomotory role. Here again the occurrence of egg-ventilation movements in *P. cometes* suggests a functional advantage for the large uropods.

As with the pontiniid prawns, detailed study of these commensal porcellanids reveals that many of the differences between related commensals can be understood as adaptations to somewhat different modes of life. The difference between the rather flat carapace of *P. cometes* and that of *P. loimicola*, which is strongly arched in an antero-posterior direction, corresponds with the difference in curvature of the tubes of the respective hosts; so also the size of these commensals agrees with the size of the host tubes.

At a much higher level of differentiation most of the peculiarities which differentiate *Pseudoporcellanella* from *Porcellana* (*Porcellanella*) are readily understood as adaptations for life on the narrow stems and bulbs of *Scytalium* in contrast to life between the flat leaves of *Pteroeides*. The body form, type of walking legs, and peculiar chelipeds are paralleled in varying degree by other porcellanids, such as *Orthochela* and *Euceramus* which are associated with narrow-stemmed gorgonians and also by members of the related family Chirostylidae which are commensal with gorgonians. It is more difficult to see the functional significance of the reduced antennal flagellum of *Pseudoporcellanella* but similar reduction occurs in *Minyoceras* and there is slight reduction in *Porcellana* (*Porcellanella*) so that one can conclude that it is in some way an adaptation for a commensal mode of life. Such a view is at least more meaningful than seeing the reduction as in some way foreshadowing the brachyuran condition.

There are other structural features of commensal porcellanids which look as though they should have adaptive value but whose function remains obscure. Such is the tendency amongst tube-dwelling commensals of the genus *Polyonyx* to develop conspicuous fringes of long matted setae. Such fringes are absent in free living members of the genus and in porcellanid commensals which live "in the open". They are present however in the unusual genus *Rhaphidopus* which lives in association with burrowing polychaetes though not as a strict commensal. Similar tendencies are shown by various groups of mud burrowing crabs and also by those crabs of the family Pinnotheridae which live in worm tubes or as endocommensals in the cloacal region of Holothuria. Thus, even though the exact function remains obscure, the convergent development of such setal fringes and coats by members of very different groups is sufficient to show that they have some functional significance.

Summary

Accounts are given of the structure and some aspects of the biology of three commensal crustaceans from Singapore. One of these represents a new genus of prawns of the subfamily Pontoniinae; the others are little known members of the family Porcellanidae.

It is suggested that the apparent rarity of these and other tropical commensal decapods is probably a spurious phenomenon resulting from inadequate collecting methods.

The functional taxonomy of these commensals is discussed and it is suggested that many of their structural peculiarities can be interpreted as adaptations to their mode of life.

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