

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

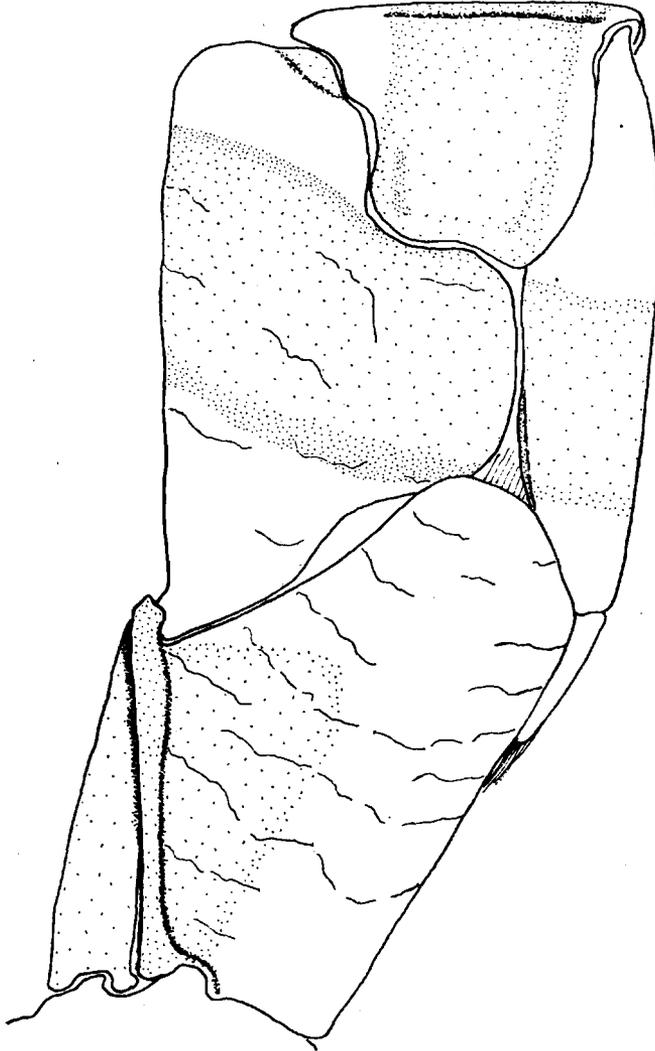


FIG. 17. *Pseudoporcellanella manoliensis* Sankarankutty. Right third maxillipede ventral view in resting position.

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.

REFERENCES

- Borradaile, L. A. (1917). On the Pontoniinae. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr J. Stanley Gardinar. *Trans. Linn. Soc. Lond. (Zool.)* (2) 17: 323-396, pls. 52-57.
- Bruce, A. J. (1965). Notes on Indo-Pacific Pontoniinae. X. *Periclimenes cristimanus* sp. nov. a new pontoniinid shrimp from Singapore. *Ann. Mag. nat. Hist.* (13) 8: 487-493.
- Cain, A. J. (1959). Function and taxonomic importance. *Publs Syst. Ass.* 3: 5-19.
- Cain, A. J. (1964). The perfection of animals. In *Viewpoints in Biology* 3: 36-63. Carthy, J. D. & Duddington, C. L. (eds). London: Butterworth.
- Gordon, I. (1960). Additional note on the porcellanid sea-anemone association. *Crustaceana* 1: 166-167.
- Haig, J. (1960). The Porcellanidae (Crustacea Anomura) of the eastern Pacific. *Allan Hancock Pacif. Exped.* 24: 1-440.
- Haig, J. (1964). Porcellanid crabs from the Indo-West Pacific Part I. Papers from Dr Th. Mortensen's Pacific Expedition 1914-1916, 81. *Vidensk. Meddr dansk naturh. Foren.* 126: 355-386.
- Holthuis, L. B. (1950). The Decapoda of the Siboga Expedition. Part XI. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species I. Subfamily Palaemoninae. *Siboga Exped.* No. 39a⁹: 1-268.
- Holthuis, L. B. (1952). The Decapoda of the Siboga Expedition. Part XI. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species II. Subfamily Pontoniinae. *Siboga Exped.* No. 39a¹⁰: 1-253.
- Johnson, D. S. (1958). The Indo-West Pacific species of the genus *Polyonyx* (Crustacea, Decapoda, Porcellanidae). *Ann. Zool., Agra* 2: 95-118.
- Johnson, D. S. (1961). A synopsis of the Decapoda Caridea and Stenopodidea of Singapore, with notes on their distribution and a key to the genera of Caridea occurring in Malayan waters. *Bull. natn. Mus. St. Singapore* 30: 44-79.
- Johnson, D. S. (1963). Commensalism and semi-parasitism amongst decapod Crustacea in Singapore waters. *Proc. First reg. Symp. sci. Knowl. trop Parasites, Singapore* 1962: 282-288.
- Johnson, D. S. (In press). The Galatheidea (Crustacea, Decapoda) of Singapore and adjacent waters. *Bull. natn. Mus. Rep. Singapore*.
- Johnson, D. S. & Liang, M. (1966). On the biology of the watchman prawn, *Anchistus custos* Forskal (Crustacea; Decapoda; Palaemonidae), an Indo-West Pacific commensal of the bivalve *Pinna*. *J. Zool., Lond.* 150: 433-455.
- Jones, S. (1959). Notes on animal associations. 1. A porcellanid crab on the sea pen, *Pteroeides esperi* Herklots. *J. mar. biol. Ass. India* 1: 178-179.
- Man, J. G. de (1888). On the podophthalmous Crustacea of the Mergui Archipelago. *J. Linn. Soc. Lond. (Zool.)* 22: 1-305.
- Manton, S. (1958a). Habits of life and evolution of body design in Arthropods. *J. Linn. Soc. Lond. (Zool.)* 44: 58-72.
- Manton, S. (1958b). Functional morphology and the evolution of diagnostic characters of arthropodan groups. *Int. Congr. Zool.* 15: 390-393.
- Manton, S. (1959). Functional morphology and taxonomic problems of Arthropoda. *Publs Syst. Ass.* 3: 23-32.
- Patton, W. K. (1966). Decapod Crustacea commensal with Queensland branching corals. *Crustaceana* 10: 271-295.
- Patton, W. K. (In press). Crustaceans as symbionts. *Symposium on Crustacea, Ernakulam, India, 1965*.

- Potts, F. A. (1915). The fauna associated with the crinoids of a tropical coral reef; with especial reference to its colour variations. *Pap. Dep. mar. Biol. Carnegie Instn Wash.* 8: 73-96, pl. 1.
- Sankarankutty, C. (1961a). On a new genus of Porcellanidae (Crustacea-Anomura). *J. mar. biol. Ass. India* 3: 92-95.
- Sankarankutty, C. (1961b). On the porcellanid crab, *Porcellanella triloba* White (Crustacea-Anomura), a commensal on sea pen; with remarks on allied species. *J. mar. biol. Ass. India* 3: 96-100.
- Sankolli, K. N. (1965). On a new species of commensal porcellanid crab, *Polyonyx loimicola* sp. nov., from India: (Crustacea, Anomura, Porcellanidae). *J. Bombay nat. Hist. Soc.* 62: 285-291.
- Sankolli, K. N. & Shenoy, S. (1965). On the occurrence of the tube-worm *Loimia medusa* (Savigny) in Bombay waters and its commensalism with a porcellanid crab. *J. Bombay nat. Hist. Soc.* 62: 316-320, pl. 1.
- Serène, R. & Romimohtarto, K. (1963). On some species of Eumedoniinae from Indo-Malayan region. *Mar. Res. Indonesia* 6: 1-14.
- Shen, C. J. (1936). Notes on the genus *Polyonyx* (Porcellanidae) with description of a new species. *Bull. Fan meml Inst. Biol.* 6: 275-287.
- Stimpson, W. (1907). Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853-1856. *Smithson. misc. Collns* 49: 1-240, pls. 1-26.
- Tiegs, O. W. & Manton, S. M. (1958). The evolution of the Arthropoda. *Biol. Rev.* 33: 255-337.
- Walker, A. O. (1887). Notes on a collection of Crustacea from Singapore. *J. Linn. Soc. Lond. (Zool.)* 20: 107-117.