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A REVIEW OF INFORMATION UPON THE CORAL HOSTS OF COMMENSAL SHRIMPS OF THE SUB-FAMILY *PONTONINAE*, KINGSLEY, 1878 (CRUSTACEA, DECAPODA, PALAEMONIDAE)

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Abstract

Recent studies on Indo-Pacific shrimps of the subfamily Pontoniinae have indicated that the vast majority of species live in permanent commensal association with another marine invertebrate. These shrimps are particularly abundant in tropical coral reefs where they may be found in association with the larger sedentary invertebrates of most phyla. Amongst these, the species associated with corals are especially conspicuous and relatively well known.

A high degree of specificity is apparent in shrimp-coral commensalism but it is only recently that attempts have been made to identify the hosts specifically. The data at present available on the host corals of the shrimps of the subfamily Pontoniinae are catalogued and the phylogeny of the coral-inhabiting species is discussed and two main sequences of morphological changes are noted. The distribution of the shrimps is intimately correlated with that of the host corals and cannot be elucidated until details of the associations over the widest possible geographical ranges are available. To this end a key to the identification of the pontoniid shrimps associated with scleractinian corals is provided.

Introduction and Historical

The coral reefs of the tropical Indo-west-pacific region provide suitable habitats for several families of caridean shrimps. Three familes are especially conspicuous for their abundance on coral reefs, the Alpheidae Randall, 1839, the Hippolytidae Bate, 1888, and the Palaemonidae Samouelle, 1819, which is represented mainly by the sub-family Pontoniinae Kingsley, 1878, The members of these families are all now known to have developed commensal habits in many cases and this way of life is especially well developed in the Pontoniinae in which nearly all species are commensally associated with a wide range of invertebrate hosts.

The first reports of pontoniid shrimps living in association with live corals were of *Oedipus superba* and *O. graminea* (Dana, 1852). These species have been

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subsequently transferred to the genus *Coralliocaris* Stimpson. Stimpson (1860) also reported further occurrences of *C. superba* and *C. graminea* in corals and recorded the presence of *C. lamellirostris* (*Jocaste* sp.) and *Harpilius depressus* (*Harpiliopsis*) also in corals.

Many subsequent workers were content to record that their material was obtained from corals and few realized the intimate nature of the association between the shrimp and the coral. Even as recently as 1931, Gardiner, referring in general to the shrimps of coral reefs, stated that "Almost none of these have any appearance of being specifically associated with corals". Borradaile (1917) and Kemp (1922) and Johnson (1961) indicated that many shrimps of the sub-family Pontoniinae were obligate, commensals and strictly associated with stony corals, but these still remained to be identified even to generic level. Holthuis (1951) reported the occurrence of *Harpiliopsis depressus* (Stimpson) in corals of the genera *porites* Gray and *Pocillopora* Gray. The first specific determination of the coral host appears to be *Acropora leptocyathus* (Brook) for specimens of *Coralliocaris superba* (Dana) obtained in the Mariana Islands (Holthuis, 1953). There were no further records until *Pocillopora eydouxi* Milne Edwards and Haime was identified as the host of *Fennera chacei* Holthuis in Maldive Islands (Bruce, 1965) but numerous records have been reported subsequently by Patton (1966). The author's collections in the Indian Ocean have enabled the coral hosts of numerous additional species of pontoniid shrimps to be identified and the details are listed below together with data concerning shrimps from various other sources.

Some pontoniid shrimps, not included in this report, have been described as facultative commensals of corals. Some of these, such as *Palaemonella rotumana* (Borradaile) Kemp and *Periclimenes spiniferus* (De Man) occupy a wide variety of ecological niches and may be found in muddy, sandy or rocky pools, amongst *Sargassum* and other algae or amongst dead or live corals. When disturbed these shrimps take refuge in the nearest cover and are therefore frequently found on coral heads in sutiable localities. Their methods of feeding are quite independant of the coral and their association is therefore little more than accidental. *Palaemonella rotumana* has been reported as associated with live *Pavona frondifera* as well as the alcyonacean *Heliopora* (Johnson, 1961).

Various species of the genus *Periclimenaeus* Borradaile, have also been reported as associated with corals. In my opinion there are no fully authenticated cases of commensal associations between *Periclimenaeus* species and corals. *Periclimenaeus* is normally associated with sponges or ascidians and these organisms commonly encrust the bases and branches of corals. These are often damaged during the collection of the host specimen, liberating the enclosed shrimps which may then be accidentally attributed to the coral host.

No studies on the biology of these commensal shrimps and their relation to their hosts have been published. It is known that the number of shrimps occurring in a single coral head may be considerable. For example, three specimens of the coral *stylophora erythraea* von Marenzeller, about 10 ins. in diameter, collected in shallow water at Anse Etoil, Mahe, seychelles Islands, in 1966, contained the following shrimps:

	Coral 85	Coral 86	Coral 87
palaemonella rotumana	2	7	3
Periclimenes spiniferus	28	86	30
Harpiliopsis beaupresi	85	14	16
Coralliocaris graminea	—	1	—
Total number of specimens.	115	108	49

There may also be great variation in the numbers of shrimps in adjacent corals. In North West Bay, Mahe, two similar colonies of *Pocillopora elongata* Dana, situated about 5 m apart were examined with the following results.

	Coral 73	Coral 74
Periclimenes spiniferus	—	10
Periclimenes mahei	—	12
Harpiliopsis beaupresi	—	50
Harpiliopsis depressus	1	—
Coralliocaris graminea	—	1
Total number of specimens	1	73

The population of *Harpiliopsis beaupresi* in Coral 74 included individuals of all sizes from post-larvae, still showing a planktonic colour pattern to fully mature adults, indicating settlement over a prolonged period. The factors controlling settlement are not known but it would appear that one coral head was attractive to several species of shrimp, while the other was not.

The shrimps associated with the oculinid coral *Galaxea fascicularis* contrast strongly with the inhabitants of the branching corals. In general only a single pair of shrimps is found in each coral head, although sometimes a few additional individuals, generally juveniles, may be found in extra large heads. A single small head of 10-12 cm diameter, however, may contain a pair of *Platycaris latirostris*, *Ischnopontonia lophos* and *Anapontonia denticauda*, as well as several individuals of the alpheid shrimp *Racilius compressus* Paulson, and each species appears to occupy its own ecological niche within the coral. *I. lophos* and *R. compressus* are strongly compressed forms that are able to move freely between the large columnar corallites. In contract, *P. latirostris* is a strongly depressed form that rarely moves from its position half way up a corallite. *A. denticauda* is a compressed but sluggish species that moves little from its position usually at the bases of the corallites and sometimes in small depression of the basal septum. In *Paratypton seibenrocki*, an associate of *Acropora* spp corals, the male and female permanently inhabit a cyst in the base of a coral colony. In this case the apertures are too small for the adult male to be able to leave the cyst, unlike the condition in the coral-gall crab *Hapalocarcinus marsupialis* (Stimpson) in which the small male can escape.

The feeding habits of pontoniid coral commensals are unknown and, while many of the larger species of *Periclimenes* are active predators, the coral-gall shrimp *Paratypton siebenrocki* is considered to be a nanno-plankton feeder (Borradaile, 1921). In this species the apertures in the cyst are so small that only micro-plankton could enter the cyst in any quantity. The morphology of the female does not show any specializations that would enable the shrimp to increase the flow of water through the cyst, indeed the exopods of the maxillipeds are reduced in comparison with most other pontoniid shrimps. The male, however, although much smaller in size than the female, has the pleopods greatly broadened and partly enclosed by the abdominal pleura which form a stiff-walled channel, a mechanism which could be used to create a water current through the cyst (Bruce, 1969 *a*).

Borradaile (1917), has also remarked that, despite the variety of hosts with which they may be commensally associated, pontoniid shrimps show little variation in the structure of the mouthparts. In general, it may be stated that the more highly adapted forms possess mouthparts that are more adapted to dealing with smaller particles than those of the less modified or free-living shrimps. My only personal observation concerns a specimen of *Platycaris* latirostris, obtained in the Seychelles Islands, which was kept in a small dish of sea water with a small part of the host colony of *Galaxea fascicularis*. After remaining in the dish overnight, the shrimp was found to have the gastric mill packed with small brown granules in the morning. These granules were indistinguishable from the zooxanthellae in the coral tissues, but it could not be ascertained whether these had been obtained from live coral tissues or from necrotic tissue resulting from handling the coral. It was also not determined if the zooxanthellae were digested as the shrimp did not survive. However the shrimp could not be induced to eat finely divided shrimp abdominal muscle tissue, copepods or *Artemia* nauplii. Specimens of *Ischnopontonia lophos* obtained at the same time, showed no signs of feeding during the short period of observation during which it survived.

As the commensal relationship between these shrimps and their coral hosts is obligatory, the shrimps are not found away from their hosts. These hosts, in addition to providing a direct or indirect source of food, also provide protection for the shrimps from predators, and shrimps that are artificially removed from their hosts are rapidly caught and eaten by such fish as *Thalassoma* sp. *Abudefduf* sp that generally abound on coral reefs. Brightly coloured species such as *Coralliocaris graminea* and *C. superba* are conspicuous once removed from their hosts and are soon eaten, but even such transparent species as *Palaemonella rotumana* are also rapidly consumed when in open water away from suitable cover. Protection of the shrimps within the coral is far from complete and the incidence of specimens with limbs undergoing regeneration is high. The loss of appendages may be caused by small predators that are also able to move freely within the coral colony such as crabs, stomatopods or small predatory fish such as eels.

In the following list the authors of published records are quoted. Those records given without references are from personal observations. Non-specific host records, such as "madrepore corals", are not included, except where no further information has become available. Personal observations confirming earlier published records are indicated by an asterisk. Some of the portions of coral hosts retained in the field for subsequent identification, proved to be too small for their determination to be considered absolutely certain. This has been especially common in the genus *Acropora*, where frequently the whole colony is necessary for a reliable identification. These specimens were frequently identified as, for example, "*Acropora* sp. cf. *A. intermedia*". In these cases, the identification has not been distinguished from "*Acropora intermedia* (Brook)", etc.

Systematic List of Host Corals and Their Associates

Scleractinia

Periclimenes parvus Borradaile 1898 (Johnson, 1961)

Thamnasteriidae Vaughan and Wells, 1943

1 *Psammocora* (*Stephanaria*) *togianensis* Umbgrove
Periclimenes diversipes Kemp
Pocilloporidae Gray, 1842
Pocillopora sp.
Periclimenes bayeri Holthuis, 1953
Periclimenes consobrinus De Man

2 *Pocillopora acuta* Lamarck
Harpiliopsis beaupresi (Audouin)

3 *Pocillopora damicornis* (L)
Vir orientalis (Dana)
Periclimenes amymone de Man, (Patton, 1966)*
Periclimenes madreporae Bruce, (Patton, 1966, as *P. inornatus*)
Harpiliopsis beaupresi (Audouin), (Patton, 1966)
Harpiliopsis depressus Stimpson
Jocaste japonica (Ortmann)

4 *Pocillopora danae* (Verrill)
Harpiliopsis beaupresi (Audouin)
Coralliocaris graminea (Dana)
Coralliocaris superba (Dana)

5 *Pocillopora elongata* Dana
Periclimenes mahei Bruce
Harpiliopsis beaupresi (Audouin)
Harpiliopsis depressus (Stimpson)
Coralliocaris graminea (Dana)

6 *Pocillopora eydouxi* Milne-Edwards and Haime
Fennera chacei Holthuis, (Bruce, 1965)
Harpiliopsis beaupresi (Audouin)
Harpiliopsis depressus Stimpson

7 *Pocillopora hemprichi* (Ehrenberg)
Periclimenes lutescens auct., (Bruce, 1971)

8 *Pocillopora ligulata* (Dana)
Harpiliopsis depressus (Stimpson), (Chace, 1937)*

9 *Pocillopora verrucosa* (Ellis and Solander)
Periclimenes madreporae Bruce, (Patton, 1966, as *P. inornatus*)
Fennera chacei Holthuis, (Patton, 1966)
Harpiliopsis beaupresi (Audouin), (Patton, 1966)*
Harpiliopsis depressus (Stimpson), (Patton, 1966)*
Joscaste lucina (Nobili), (Patton, 1966)

10 *Pocillopora woodjonesii* Vaughan
Harpiliopsis beaupresi (Audouin)
Harpiliopsis depressus (Stimpson)

11 *Seriatopora angulata* Klunzinger
Harpiliopsis depressus (Stimpson)

12 *Seriatopora hystrix* (Dana)
Periclimenes amymone de Man, (Patton, 1966)*
Periclimenes lutescens auct., (Patton, 1966)
Periclimenes madreporae Bruce, (Patton, 1966, as *P. inornatus*)*
Harpiliopsis beaupresi (Audouin), (Patton, 1966)*
Harpiliopsis depressus (Stimpson). Patton, 1966)

13 *Stylophora erythraea* von Marenzeller
Vir orientalis Dana
Periclimenes diversipes Kemp
Harpiliopsis beaupresi (Audouin)
Coralliocaris graminea (Dana)

14 *Stylophora mordax* (Dana)
Periclimenes amymone de Man, (Patton, 1966)
Periclimenes madreporae Bruce, (Patton 1966 as=*P. inorantus*)

Harpiliopsis beaupresi (Audouin)
Harpiliopsis depressus (Stimpson), (Patton, 1966)*

15 *Stylophora pistillata* (Esper)
Vir orientalis (Dana)
Periclimenes amymone de Man (Patton, 1966)*
Periclimenes madrepora Bruce, (Patton, 1966 as=*P. inorratus*)*
Harpiliopsis beaupresi (Audouin)
Harpiliopsis depressus (Stimpson), Patton, 1966)*

Acroporidae Verrill, 1902
Acropora sp.
Periclimenes diversipes Kemp, (Patton, 1966)
Periclimenes madreporae Bruce, (Patton 1966, as *P. inornatus*)
Philarius imperialis Kubo, (Patton, 1966)*
Philarius lifuensis (Borradaile)
Harpiliopsis beaupresi (Audouin)
Harpiliopsis depressus (Stimpson)
Cavicheles kempi Holthius, (Bruce, 1966a)

16 *Acropora conferta* (Quelch)
Jocaste lucina (Nobili), Bruce, 1969*a*)

17 *Acropora convexa* (Dana)
Periclimenes lutescens auct., (Bruce, 1971)
Coralliocaris venusta Kemp
Joscaste japonica (Ortmann), (Bruce, 1969*b*)

18 *Acropora corymbosa* (Lamarck)
Periclimenes madreporae Bruce
Coralliocaris brevirostris Borradaile
Coralliocaris graminea (Dana)
Jocaste lucina (Ortmann), Bruce, 1969*b*)[1]

19 *Acropora cuneata* (Dana)
Periclimenes madreporae Bruce
Jocaste lucina (Ortmann), Bruce, 1969*b*)

20 *Acropora cymbicyathus*
Periclimenes amymone De Man
Coralliocaris graminea (Dana)
Coralliocaris superba (Dana)

1. Possibly from *A. spicifera* (Dana)

21 *Acropora digitifera* (Dana)
Periclimenes amymone de Man
Periclimenes madreporae Bruce
Philarius gerlachei (Nobili)[2]
Jocaste japonica (Ortman), (Bruce, 1969*b*)
Coralliocaris nudirostris (Heller)
Coralliocaris superba (Dana)
Coralliocaris venusta Kemp[2]

22 *Acropora diversa* (Dana)
Periclimenes amymone De Man
Jocaste japonica (Ortmann), Bruce, 1969*b*)
Corelliocaris graminea (Dana)
Coralliocaris superba (Dana)

23 *Acropora eurystoma* (Klunzinger)
Periclimenes amymone De Man
Coralliocaris superba (Dana)

24 *Acropora formosa* (Dana)
Philarius gerlachei (Nobili)

25 *Acropora haimei* (Milne-Edwards and Haime)
Jocaste japonica (Ortmann), (Bruce, 1969*b*)
Coralliocaris graminea (Dana)

26 *Acropora hebes* (Dana)
Jocaste lucina (Nobili), Bruce, 1969*b*)
Coralliocaris graminea (Dana)

27 *Acropora humilis* (Dana)
Periclimenes lutescens auct.
Philarius gerlachei (Nobili)[3]
Jocaste japonica (Ortmann), Bruce, 1969*b*)
Jocaste lucina (Nobili), (Bruce, 1969*b*)
Coralliocaris graminea (Dana)
Coralliocaris superba (Dana)
Coralliocaris brevirostris Borradaile
Coralliocaris nudirostris (Heller)
Coralliocaris venusta Kemp[3]

28 *Acropora hyacinthus* (Dana)
Periclimenes amymone De Man
Philarius gerlachei (Nobili)

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2. Possibly from *A. humilis* (Dana)
3. Possibly from *A. digitifera* (Dana)

Paratypton siebenrocki Balss, (Bruce, 1969*a*)
Coralliocaris brevirostris Borradaile

29 *Acropora irregularis* (Brook)
Jocaste lucina (Nobili), (Bruce, 1969*b*)
Coralliocaris superba (Dana)

30 *Acropora kenti* (Brook)
Periclimenes amymone De Man
Periclimenes lutescens auct.

31 *Acropora leptocyathus* (Brook)
Coralliocaris superba (Dana), (Holthuis, 1953)

32 *Acropora nana* (Studer)
Philarius gerlachei (Nobili)
Jocaste joporica (Ortmann), Bruce, 1969*b*)
Coralliocaris graminea (Dana)
Coralliocaris superba (Dana)

33 *Acropora nasuta* (Dana)
Periclimenes madreporae Bruce
Jocaste japonica (Ortmann), (Bruce, 1969*b*)
Coralliocaris graminea (Dana)

34 *Acropora palifera* (Lamarck)
Jocaste lucina (Nobili), (Bruce, 1969*b*)

35 *Acropor palmeri* Wells
Paratypton siebenrocki Balss, (Bruce, 1969*a*)

36 *Acropora paniculata* Verrill
Periclimenes lutescens auct.

37 *Acropora pulchra*
Coralliocaris superba (Dana)

38 *Acropora ramiculose* (Dana)
Jocaste lucina (Nobili), (Bruce, 1969*b*)
Coralliocaris graminea (Dana)

39 *Acropora rotumana* (Gardiner)
Periclimenes madreporae Bruce
Jocaste japonica (Ortmann), (Bruce, 1969*b*)

40 *Acropora sarmentosa* (Brook)
Periclimenes amymone De Man

41 *Acropora squamosa* (Brook)
Paratypton siebenrocki Balss (Patton, 1966), (Bruce, 1969*a*)
Jocaste japonica (Ortmann), (Bruce, 1969*b*)
Joscate lucina (Nobili), (Bruce, 1969*b*)
Coralliocaris graminea (Dana)

42 *Acropora squarrosa* (Ehrenberg)
Paratypton siebenrocki Balss, (Bruce, 1969*b*)

43 *Acropora syringodes* (Brook)
Periclimenes amymone De Man

44 *Acropora tenuis* (Dana)
Periclimenes amymone De Man
Periclimenes diversipes Kemp.
Jocaste japonica (Ortmann), (Burce, 1969*b*)
Jocaste lucina (Nobili), Bruce, 1969*b*)
Jocaste lucina (Nobili)

45 *Acropora teres* verrill
Jocaste lucina (Nobili)

46 *Acropora variabilis* (Klunzinger)
Harpiliopsis beaupresi (Audouin)
Jocaste japonica (Ortmann), (Bruce, 1969*b*)
Jocaste lucina (Nobli), (Bruce, 1969*b*)
Coralliocaris graminea (Dana)

47 *Montipora circumvallata* (Ehrenberg)
Periclimenes diversipes Kemp, (Bruce, 1971)
Agriciidae Gray, 1847

48 *Pavona danai* (Milne-Edwards and Haime)
Periclimenes diversipes Kemp

49 *Pavona divaricata* (Lamarck)
Coralliocaris pavonae (Bruce, 1972*b*)*

50 *Pavona minor* Brueggemann
Coralliocaris pavonae Bruce
Fungiidae Dana, 1846

51 *Fungia* sp.
Mesopontonia fungiacola Bruce, 1967
Poritidae Gray 1842

52 *P. diversipes* Kemp

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* Inserted in proof stage

53 *Goniopora stokesi* Milne-Edwards and Haime
Hamopontonia corallicola Bruce, 1970

54 *Porites* sp.
Harpiliopsis depressus (Stimpson), Holthuis, 1951)

55 *Porites* (*Synaraea*) *iwayamaensis* Eguchi
Periclimenes diversipes Kemp

56 *Porites* n.sp. 1, cf. *P. andrewsi* Vaughan
Periclimenes diversipes Kemp

57 *Porites* n. sp. 2
Periclimenes diversipes Kemp
Oculinidac Gray 1847

58 *Galaxea clavus* (Dana)
Periclimenes diversipes Kemp, (Bruce, 1972*a*)

59 *Glaxea fascicularis* (L)
Anapontonia denticauda Bruce, 1967
Ischnopontonia lophos (Barnard), Bruce, 1969 *a*)
Platycaris latirostris Holthuis, (Bruce, 1966*b*)
Dendrophylliidae

60 *Turbinaria*
Periclimenes madreporae Bruce

THE PHYLOGENY OF THE PONTONIINID CORAL COMMENSALS

The coral-inhabiting genera of the Pontoniinae consists of two major groups- The first group, characterized mainly by progressive loss of morphological characteristics, including gradual reduction of the exopod of the third maxilliped, of the size of the second pereiopods, and the telson spines, with simple, unspecialized dactyls on the third pereiopods and the general absence of a hepatic spine, or, if a hepatic spine is present, the presence of a long slender finger-like median process on the fourth thoracic sternite, contains the genera *Vir*, *Philarius*, *Periclimenes* (partim) *Platycaris*, *Ischnopontonia*, *Anapontonia*, *Metapontonia* and *Paratypton*. The second group is characterized generally by the presence of specially modified dactyls on the ambulatory pereiopods and the presence of a hepatic spine, and includes *Periclimenes* (partim) *Harpiliopsis*, *Fennera*, *Cavicheles*, *Coralliocaris* and *Jocaste*.

The most primitive genus of the Pontoniinae is *Palaemonella* Dana in which. a strong spine on the fourth thoracic sternite is present and also a mandibular palp, features also shared with the majority of shrimps of the Palaemoniinae. Some species of the genus *Periclimenes* (*P. amymone*, *P. consobrinus* and *P. lutescens*) only differ from *Palaemonella* at generic level by the loss of the mandibular palp. *Vir* is also closely related to *Palaemonella* but has a depressed body form and has also lost the hepatic spine. *Philarius* has a depressed body form similar to *Vir* but has also lost the mandibular palp and is closely related therefore to the species of *Periclimenes* with a fourth thoracic sternal spine, differing from them only in the loss of the hepatic spine. In the further evolution of this group the fourth thoracic sternal spine is suppressed and there is a progressive tendency towards the reduction of spiny processes, including the rostrum and scaphocerite, with the adoption of increasingly cryptic habits. At the same time some specialized adaptions to specifilized habits are developed. *Platycaris* is related to *Philarius* but carpace and rostral spines are absent and an extremely flattened body form has been developed. *Ischanopontonia* and *Anapontonia* are also related to *Philarius*, retaining moderately developed toothed rostra, but have developed strongly compressed body form with specialized holdfast mechanisms on the uropods. In *Anapontonia* the exopod of the third maxilliped has undergone reduction and the dorsal telson spines are absent. In *Ischanopontonia* the endite of the maxilla is small compared with *Vir* and *Philarius* and in *Anapontonia* and *Metapontonia* the endites are quite absent. *Paratypton* is the most higly modified genus of the group and occupies the most restrictive habitat. The rostrum has been completely suppressed and the scaphocerite reduced to a small lamina. In addition to the total absence of the expod of the third maxilliped, that of the second is also absent. The endite of the maxilla is also absent. The second pereiopods are also most markedly reduced and the telson spines minute.

The second group of genera includes those species of *Periclimenes* without a median process on the foruth thoracic sternite, (*P. diversipes*, *P. madreporae*, *P. mahei*) which are the most primitive of this section and most closely related to the palaemonid stock. In these species the dactyls of the ambulatory pereiopods are simple and have not undergone any specialization in association with the host in which they live. This may account for *P. diversipes* being the species found with the widest variety of hosts. In *Harpiliopsis* specialization of the dactyls takes the form of strong marginal cariane and a squamous ventral surface. *Fennera* has developed a small rounded basal process and *Cavicheles* a large acute squamose process. The most extreme form of basal process is found in the genera *Coralliocaris* and *Jacaste* which have evolved a robust, hoof-shaped process, surmounted by a small hooked unguis. In *Coralliocaris* the hepatic spine is lost but the chelae of the second pereiopods are robust and similar, and in some species the rostrum has undergone marked reduction. In *Jocaste* the hepatic spine is retained and the rostrum is normally developed but the chelae of the second pereiopods are quite dissimilar, the minor chela being a specialized subspatulate scoop.

A key to the identification of the shrimps known to be definitely associated with Indo-Pacific corals is provided. Detailed description of most of the species concerned are to be found in the reports by Kemp (1922) and Holthuis (1952).

The species *Periclimenes parvus* Borradaile is not included in the key and the association with corals based on a single specimen (Johnson, 1969), requires verification It is probable that *Periclimenes lutescens* auct. is distinct from *P. lutescens* (Dana) and it is likely that many further species of pontoniid shrimp remain to be discovered, especially in corals from greater depths on the coral reefs as observations have so far been mainly based on corals that are exposed at low water or in shallow depths. Many corals have not yet been found to harbour shrimps but many genera still remain to be examined. For example Stephenson, *et al*, (1931) has reported the presence of shrimps on corals of the genus *Euphyllia* but as yet none have been identified and it is uncertain to which family of the Caridea they may belong.

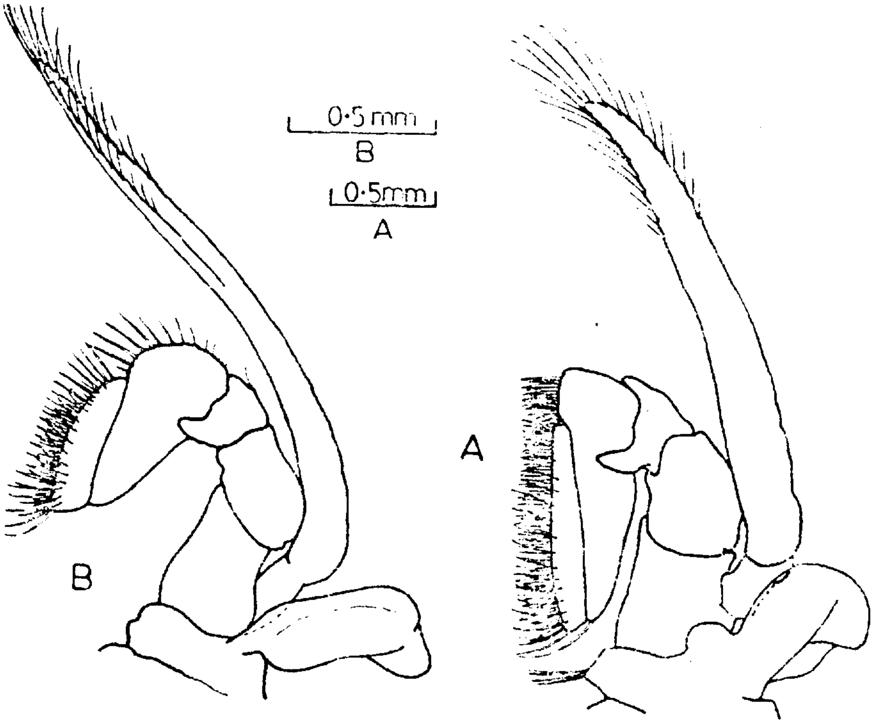

Fig. 1 Second maxillipeds of A) *Periclimenes lutescens* auct. and B) *Periclimenes consobrinus* De Man.

A Key to the Indo-West-Pacific Pontoniinid Shrimps Associated with Scleractinian Corals

1.	A finger-like median process present on the fourth thoracic sternite	2
	No median finger-like process on fourth thoracic sternite	8
2.	Mandibular palp present	*Vir orientalis* (Dana, 1852)
	Mandibular palp absent	3
3.	Hepatic spine present	4
	Hepatic spine absent	6

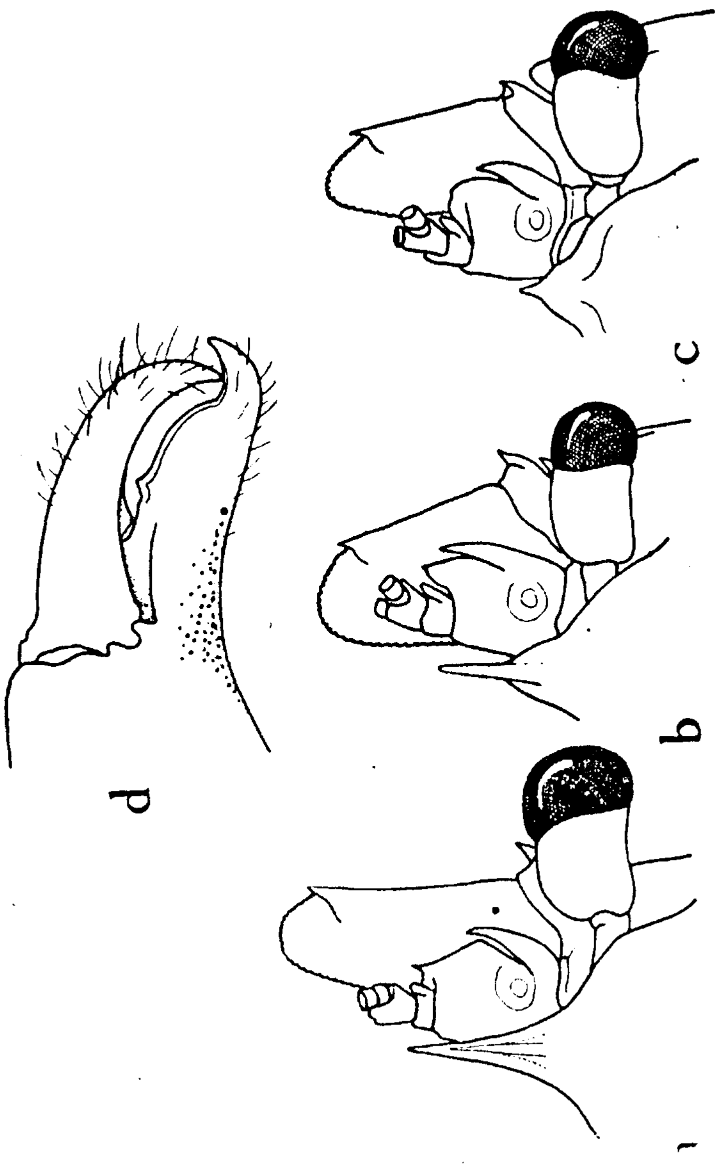

Fig. 2 Dorsal view of rostrum, anterior carapace, antennular peduncle and scaphocerite of a) *Coralliocaris macrophthalma* (H. Milne Edwards), Saya de Malha, 26 fms., ovigerous female b) *Coralliocaris nudirostris* (Heller), Goifurfehndu Atoll, Maldive Islands. c) *Coralliocaris brevirostris* Borradaile, holotype, female, Funafuti, d) fingers of second pereiopod of *Coralliocaris brevirostris* Borradaile. (Specimens in the collection of the Zoological Museum, Cambridge.)

4. Supra-orbital spine present *Periclimenes amymone* De Man, 1902

 Supra-orbital spine absent 5

5. Medial border of distal and penultimate segments of expod of second maxilliped forming a continuous border, fringed with setae. *Periclimenes lutescens* auct.

 Medial border of penultimate segment of endopod of second maxilliped not forming a continuous border with distal segment. *Periclimenes consobrinus* De man, 1902

6. Posterior rostral teeth situated on anterior carpace; carpus of second pereiopod with disto-lateral spine. *Philarius imperialis* (Kubo, 1940)

No teeth situated on carapace; carpus of second pereiopod unarmed. 7

7. Supra-orbital spine present. *Philarius lifuensis* (Borradailc,, 1878)
Supra-orbital spine absent. *Philarius gerlachei* (Nobili, 1905)

8. Dactyls of ambulatory pereiopods simple, without carinae or basal processes or protruberances 9

Dactyls of ambulatory pereiopods carinate or with basal processes 17

9. Hepatic spine present 10
Hepatic spine absent 12

10. Chelae of second pereiopod subequal, similar 11
Chelae of second pereiopods markedly dissimilar, unequal *Periclimenes diversipes* Kemp, 1922

11. Fingers of second pereiopods strongly toothed proximally and cutting edges concave gaping distally *Periclimenes mahei* Bruce, 1969b

Fingers of second pereiopods feebly dentate, without gaping concave cutting edges distally. *Periclimenes madreporae* Bruce, 1969b

12. Rostrum absent; scaphocerite greatly reduced *Paratypton siebenrocki* Balss, 1915

Rostrum present; scaphocerite normal 13

13. Body normal, neither compressed nor depressed; telson without terminal spines, a pair of hook-like process present on posterior border of telson. *Hamopontonia corallicola* Bruce, 1969

Body compressed or depress; three pairs of posterior telson spines present 14

14. Body strongly depressed; rostrum toothless; hepatic and antennal spines absent. *Platycaris latirostris* Holthuis, 1952

Body compressed 15

15. Rostral lamina short, toothless, with a single large trianular tooth on anterior carapace *Metapontonia fungiacola* Bruce, 1967

Rostral lamina and anterior carapace dorsally dentate 16

16. Body moderately compressed; second pereiopods feebly developed; telson without dorsal spines; lateralborder of exopod of uropod strongly dentate *Anapontonia denticauda* Bruce, 1967

Body strongly compressed; second pereiopods well developed, articulating in a vertical plane; dorsal telson spines present; lateral border of exopod of uropod with large hooked spine *Ischnopontonia lophos* (Barnard, 1962)

17. Dactyls of ambulatory pereiopods with dorsal and dorso-lateral carinae but without basal processes 18

Dactyls of ambulatory pereiopods with basal process, non-carinate 19

18. Hepatic, antennal and lateral spine of basicerite in straight line; outer margin of second pereiopod concave, ventral surface carinate *Harpiliopsis beaupresi* (Audouin, 1825

Hepatic, antennal and lateral spine of basicerite not in line, antennal spine close to inferior orbital angle; outermargin of dactylus of second pereiopod convex, ventral surface not carinate *Harpiliopsis depressus* (Stimpson, 1860)

19. Basal process of dactyls of ambulatory pereiopods rounded or pointed, not hoof shaped 20

Basal process of dactyls of ambulatory pereiopods hoof shaped, not rounded or pointed 21

20. Basal processes of dactyls of ambulatory pereiopods small and rounded; a row of 3-5 spines present along orbital margin posterior to antennal spine *Fennera chacei* Holthuis, 1951

Basal processes of dactyls of ambulatory pereiopods with large, squamose, acute process; orbital margin non-spinose *Cavicheles kempi* Holthuis, 1952

21. Hepatic spine present; chelae of second pereiopods markedly dissimilar 22

Hepatic spine absent; chelae of second pereiopods similar 23

22. Supra-orbital margin angulate; rostrum with 4-7 dorsal and 1-4 ventral teeth, generally 5/2-3; dactyl of major second periopod with two teeth on cutting edge *Jocaste lucina* (Nobili, 1901)

Supra-orbital margin convex; rostrum with 3-5 dorsal and 1-2 ventral teeth, generally 4/1; dactyl of major second pereiopod with one teeth on cutting edge *Jocaste japonica* (Ortmann, 1890)

23. Chela of second pereiopods with large molar process on fixed finger, outer margin of dactylus semicircular 24

Chela of second pereiopod without molar process on fixed finger, outer margin of dactylus not semicircular 25

24. Rostrum with 4-6 dorsal and 1-2 ventral teeth. *Coralliocaris graminea* (Dana, 1850)
Rostrum with 1 dorsal and O ventral teeth; *Coralliocaris macrophthalma* (H. Milne Edwards, 1837) (Fig. 2a)

25. Dactylus of second pereiopod ventrally carinate or with proximal protruberance 26

Dactylus of second pereiopod not ventrally carinate or with proxinal protruberanc 28

26. Fixed figner of second pereiopod with a distinct oval fossa on proximal part of cutting edge *Coralliocaris pavonae* Bruce, 1972

Fixed fingers of second pereiopods without a distinct fossa on cutting edge 27

27. Rostrum with 4-5 dorsal and 2 ventral teeth; second pereiopod with dactylar basal protruberance distinctly angulated *Coralliocaris superba* (Dana, 1852)

Rostrum with 0-2 dorsal and 0-1 ventral teeth; second pereiopod with dactylar basal protruberance gently rounded *Coralliocaris venusta* Kemp, 1922

28. Basal segment of antennular peduncle as long as wide, with well developed antero-lateral lobe bearing an acute disto-lateral spine; rostrum reaching to middle of intermediate segment of peduncle *Coralliocaris nudirostris* (Heller, 1861) (Fig. 2 b)

Basal segment of antennular peduncle wider than long, with feebly developed anterolateral lobe bearing an obsolescent distolateral spine; rostrum extending only to middle of basal segment of peduncle.

(*Coralliocaris brevirostris* Borradaile, 1898.)
(Fig. 2 c)

SUMMARY

The information on the shrimps of the sub-family Pontoniinae, Kingsley, 1878, so far known to be obligate commensals of scleractinian corals, is listed. Sixty corals, of twelve genera, have been identified as hosts for thrity species of pontoniid shrimp belonging to fourteen genera. The coral hosts are limited to the families Thamnasteridae, Pocilloporidae, Acroporidae, Agariciidae, Fungiidae, Poritidae, Oculinidae and Dendovphylliidae.

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