Coral Reef Caridea and "Commensalism"[1]

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Introduction

The purpose of this paper is to provide a general review of what is presently known about the "commensal" caridean shrimps found in the coral reef biotope. The information is based largely upon the available literature and studies carried out in the western Indian Ocean, but the findings in this region probably apply extensively to the rest of the Indo-West Pacific region and also, to a lesser extent, to coral reef regions of the Eastern Pacific and Atlantic Oceans.

The nature of the associations between many tropical caridean shrimps and other marine animals, for which the term "commensalism" is frequently used, is at present little understood and largely uninvestigated. It is probable, in view of the wide variety of animals involved, that a variety of different mechanisms may be involved. The term commensal is used in this paper only in a general sense to indicate the existence of a specific link between a shrimp and another marine animal, so that the former is generally to be found only in association with the latter, and not to imply any precise trophic relationship between the two organisms.

Many of the first tropical coral reef shrimps to be described were recorded without their associations with other marine animals being appreciated, although the existence of commensalism amongst shrimps had been known for a long time in the case of some Mediterranean species. One of the earliest tropical examples was noted by Rumphius (1705), who reported the occurrence of shrimps in *Tapes litterata* (Holthuis, 1952), and these shrimps have never been seen since. Details of these shrimp associations were gradually accumulated and can be traced through the reviews given by Borradaile (1917), Kemp (1922), Balss (1966) and Holthuis (1952). More recently Patton (1966) has provided a general account of commensalism in the crustacea, including shrimps. Many of the species of commensal shrimp are small or cryptically coloured and liable to be easily overlooked unless specially searched for. Shallow-water species involved with corals or molluscs were generally the first to be definitely linked with their hosts (Dana, 1852; Peters, 1852), whereas material obtained by dredge or trawl from deeper water was probably often separated from its host in the process of collection. In recent years the common use of the aqualung has proved an ideal means of making precise

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Fig. 1. *Periclimenes imperator* Bruce, male and female on an unidentified host found swimming beneath the sea surface off Heron Island, Queensland, Australia. From a colour photograph by Valerie Taylor.

Table 1. The associations between Indo-West Pacific caridean shrimp genera and their hosts. The shrimp genera may also contain other species that are not known to be commensals or are considered to be free-living.

	PONTONIINAE	*ALPHEIDAE*	*HIPPOLYTIDAE*	*OTHERS*
1. *PORIFERA*	*Periclimenes* *Thaumastocaris* *Periclimenaeus* *Onycocaris* *Typton* *Anchistioides*	*Synalpheus* *Alpheus*	*Gelastocaris* *Hippolysmata*	*Discias*
2. *COELENTERATA*				
a) Hydroida	*Periclimenes*		*Hippolyte* *Thor*	
b) Milleporina	*Hamodactyloides*		*Thor*	
c) Scyphozoa	*Periclimenes*		*Latreutes*	
d) Alcyonacea	*Periclimenes* *Propontonia* *Hamodactylus*	*Synalpheus* *Alpheus*	*Hippolyte*	

Table 1. (continued)

e)	Gorgonacea	*Periclimenes* *Mesopontonia* *Hamodactylus* *Pontonides*			
f)	Pennatulacea	*Dasycaris*	*Synalpheus* (?)		
g)	Telestacea	*Periclimenes* *Hamodactylus*	*Synalpheus*		
h)	Actiniaria	*Periclimenes*		*Thor*	
i)	Coralliomorpha	*Pliopontonia*			
j)	Scleractinea	*Vir* *Periclimenes* *Philarius* *Hamopontonia* *Ischnopontonia* *Anapontonia* *Metapontonia* *Platycaris* *Fennera* *Tectopontonia* *Cavicheles* *Jocaste* *Coralliocaris* *Paratypton* *Harpiliopsis*	*Alpheus* *Synalpheus* *Racilius*	*Thor*	
k)	Antipatharia	*Dasycaris* *Pontonides*			
3.	*ANNELIDA*				
	Polychaeta		*Salmoneus* (?)		
4.	*MOLLUSCA*				
a)	Pelecypoda	*Anchitus* *Paranchistus* *Conchodytes* *Platypontonia* *Chernocaris*			
b)	Gastropoda	*Periclimenes*			
5.	*CRUSTACEA*				
	Paguridea		*Aretopsis*		
6.	*ECHINODERMATA*				
a)	Asteroidea	*Periclimenes*			
b)	Echinoidea	*Periclimenes* *Allopontonia* *Tulearіocaris* *Stegopontonia*	*Pterocaris* (?) *Athanas*		*Gnathophylloides* *Levicaris*
c)	Ophiuroidea	*Periclimenes*			
d)	Holothuroidea	*Periclimenes* *Conchodytes*			*Pycnocaris*
e)	Crinoidea	*Palaemonella* *Periclimenes* *Parapontonia* *Araiopontonia* (?) *Pontoniopsis*	*Synalpheus*		
7.	*CHORDATA*				
a)	Ascidiacea	*Periclimenaeus* *Dasella* *Pontonia*	*Synalpheus*		
b)	Pisces		*Alpheus*	*Lysmata*	*Leandrites*

collections of subtidal animals and has produced much of the information upon which this report is based.

The Shrimp—Host Associations

The shrimps and prawns found on tropical reefs belong to two main groups. The Stenopodidea are represented by one family with three genera only in shallow water and are probably all free-living, although some are involved in cleaner associations with fish. The Caridea are a much larger group, with numerous families and many genera, which dominate the coral reef shrimp fauna. Three taxa are particularly conspicuous in this habitat, the subfamily Pontoniinae and the families Alpheidae and Hippolytidae, all of which contain many species with commensal associations involving members of most of the marine invertebrate phyla with large benthic species. These associations are now briefly reviewed.

Sponges are hosts for a variety of pontoniine shrimp genera. These include particularly the large genus *Periclimenaeus* Borradaile (of which some species are found in tunicates) as well as *Onycocaris* Nobili and the monospecific genus *Thaumastocaris* Kemp. All these occur within cavities in the sponge tissues. Some species of the genus *Periclimenes* Costa such as *P. incertus* Borradaile are to be found on the external surfaces of the sponge host. Also found in sponges is the aberrant genus *Anchistioides* Paulson. Two alpheid genera are frequently represented in associations with sponges, primarily *Synalpheus* Bate and to a lesser extent *Alpheus* Fabricius. The hippolytid shrimps are less conspicuous as sponge commensals but the shrimp *Gelastocaris paronae* Nobili is noteworthy. Other hippolytids belonging to *Hippolysmata* Stimpson are also found on the outer surfaces of some branched sponges. The small family Disciadidae, with only the single genus *Discias* Rathbun, contains shrimps that live in small cavities just beneath the surfaces of sponges.

Coelenterates are hosts for the greatest variety of tropical shrimps and these associations are of special interest in view of the apparent immunity of the shrimp to the action of the host's nematocysts. The greatest variety of genera are found in association with the scleractinian corals, especially the forms with complex branching such as *Acropora, Seriatopora, Stylophora* and *Pocillopora.* The associations often involve a high degree of specificity. The pontoniine genera *Vir* Holthuis, *Periclimenes, Fennera* Holthuis, and *Harpiliopsis* Borradaile are generally associated with pocilloporid corals, while *Jocaste* Holthuis, *Coralliocaris* Stimpson, *Philarius* Holthuis, *Tectopontonia* Bruce and *Periclimenes* are commensals of acroporid corals. The remarkable pontoniine *Paratypton siebenrocki* Balss is also an associate of *Acropora* and forms a cyst within the corallum that communicates with the exterior only through a few minute apertures. Male and female are permanently incarcerated together in this small cavity which often shows subdivision into a larger and a smaller chamber apparently occupied by the female and the male respectively. Massive hermatypic corals such as *Goniopora* are also hosts for some pontoniines of the genera *Periclimenes* and *Hamopontonia* Bruce. Fungid corals such as *Fungia* and *Parahalometra* are hosts for *Metapontonia fungiacola* Bruce,

which also occurs on the faviid coral *Hydnophora*. The oculinid coral *Galaxea fascicularis* is host for three shrimps belonging to monospecific pontoniine genera, *Anapontonia denticauda* Bruce, *Ischnopontonia lophos* (Barnard) and *Platycaris latirostris* Holthuis, together with an alpheid *Racilius compressus* Paulson. Other alpheids may also be found in branching corals such as the well known orange-red *Alpheus lottini* Guerin and the scarlet *Synalpheus charon* Heller found on *Stylophora* and *Pocillopora*. The hippolytids are much less well represented and only *Thor spinosus* Boone and *T. amboinensis* De Man seem to be truly associated with corals. Ahermatypic corals may also act as hosts for shrimps, such as *Dendrophyllia micracantha* for *Pontonides maldivensis* (Borradaile). Several of the corals that are hosts for shrimps, particularly those of a non-branching habitus, have their polyps expanded by day, *i.e.*, *Galaxea fascicularis, Goniopora* spp. and *Fungia actiniformis*. Many corals that would appear to be suitable hosts for shrimp have so far failed to provide any associates, although further examination may well reveal their presence. For example, the oculinid *Acrhelia horrescens*, the mussids *Lobophyllia*, or *Symphyllia* and the caryophyllids *Euphyllia* or *Plerogyra* have yet to provide shrimp associates.

Other zoantharian orders are also known as hosts for shrimps. The Actiniaria are well known hosts for several species of *Periclimenes*. Especially well known is the association between the brightly coloured shrimp *Periclimenes brevicarpalis* Schenkel and anemones of the genus *Stoichactis*, which seem to occur on almost all tropical reefs. Species of *Periclimenes* are found also on a variety of other large anemones such as *Physobranchia* and *Radianthus*, and the genus *Pliopontonia* Bruce contains a single species, *P. furtiva*, that is found on the small coralliomorph anemone *Rhodactis rhodostoma*. The hippolytid *Thor amboinensis* is also often found on giant anemones. Antipatharians have provided few shrimps so far, all belonging to the two genera, *Dasycaris* Kemp on *Cirripathes* and *Pontonides* Borradaile on *Cirripathes* and *Antipathes*. No alpheid or hippolytid shrimp have been found on antipatharians.

Four other orders of the Anthozoa have been found involved in shrimp associations. The Alcyonacea have been found involved in associations with *Periclimenes* spp. as well as *Hamodactylus* Holthuis and *Propontonia* Bruce, in the Pontoniinae; *Alpheus* and *Synalpheus* in the Alpheidae and with *Hippolyte commensalis* Kemp, in the Hippolytidae, which is often found on *Xenia* in shallow fringing lagoons. The Gorgonacea have pontoniine associates belonging to four different genera, *Periclimenes, Mesopontonia* Bruce, *Hamodactylus* and *Pontonides,* but none belonging to the Alpheidae or Hippolytidae. *Periclimenes psamathe* (De Man) is a particularly beautiful species with very long slender appendages, with a highly transparent body with red markings, that is commonly found on a variety of small bushy gorgonians and antipatharians of the reef front. Pennatulaceans act as hosts for *Dasycaris* and also for an alpheid of the genus *Synalpheus*. The fourth order, the Telestacea, has also been found to act as host for some species of *Periclimenes* and *Hamodactylus* that also occur on gorgonians, and some *Synalpheus*

species are commonly found in the forms that have a hollow stem with openings.

The non-anthozoan coelenterates provide comparatively few instances of commensal shrimp associations, but some are rather remarkable. The shrimp *Periclimenes holthuisi* Bruce is found on the oral surface of the scyphozoan jellyfish *Cassiopia* and a hippolytid shrimp, *Latreutes anoplonyx* Kemp, is also reported to be associated with medusae. In the Hydroida, *Periclimenes galene* Holthuis is found on the hydroid *Aglaophenia cupressina*, often with the hippolytid *Hippolyte commensalis*. The shrimps of the pontoniine genus *Hamodactyloides* Fujino may be found in colonies of *Millepora* spp., often with the hippolytids *Thor spinosus* and *T. amboinensis*.

The annelids are without any proven associations with shrimps. However, Edmondson (1946) has suggested that the alpheid *Salmoneus* Holthuis may be associated with the polychaete worms *Eurythoe* spp., commonly found beneath loose slabs of dead coral on the reef flat. This association has not been confirmed.

In the Mollusca, the Pelecypoda are hosts for five genera of pontoniine shrimps, but no alpheids or hippolytids are associated with bivalves or other molluscs. The shrimp genera are *Anchistus* Borradaile, *Paranchistus* Holthuis, *Conchodytes* Peters, *Chernocaris* Johnson and *Platypontonia* Bruce; and the hosts are from the families Pinnidae, Pectinidae, Ostreidae, Tridacnidae, and Spondylidae. The shrimp *Periclimenes imperator* Bruce is an associate of nudibranch molluscs, particularly *Hexabranchus* spp., on which it is found in pairs. It has also been found on other nudibranchs and on holothurians.

Only a single example of an association between a shrimp and another decapod crustacean is so far known. The alpheid shrimp *Aretopsis amabilis* De Man is found in pairs occupying the proximal whorl of the gastropod shells occupied by large hermit crabs such as *Dardanus megistos* Herbst or *D. guttatus* Olivier, a habitat that it shares with the mysid *Heteromysis harpax* Hilgendorf, the amphipod *Gitanopsis paguri* Myers, and an isopod, *Bagatus* sp.

The Echinodermata provide a wealth of shrimp associations, all classes having some commensal shrimps, although none are from the family Hippolytidae. The Asteroidea only has associated with it some species of *Periclimenes, P. soror* Nobili being common and widespread throughout the whole Indo-West Pacific region, with *P. novercа* Kemp and *P. parasiticus* Borradaile also occurring.

The echinoids are host for many shrimps. In the Pontoniinae four genera of associates occur—*Periclimenes, Allopontonia* Bruce, *Tulеariocaris* Hipeau-Jacquotte and *Stegopontonia* Nobili. In the Alpheidae several species of *Athanas* Leach are associated and the bizarre shrimp *Pterocaris typica* Heller is also reported as an echinoid associate (Coutière, 1899). The small family Gnathophyllidae contains six genera, of which two are found in the spines of urchins, *Gnathophylloides* Schmitt and *Levicaris* Bruce.

The small ophiuroids which abound in many shallow tropical lagoons have not provided any evidence of shrimp associates. Many ophiuroids are found under stones on reef flats with a variety of alpheid shrimps, particularly *Athanas* spp., but

the ecological relationships of this small community have not been established. The larger ophiuroids belonging to the Gorgonocephalidae and Euryalidae are often hosts for the shrimp *Periclimenes lanipes* Kemp, but no others have been reported.

The Holothuroidea have also provided hosts for few commensal shrimps. *Periclimenes imperator* has been found on a small variety, and the gnathophyllid shrimp *Pycnocaris chagoae* Bruce is also found on a holothurian. *Conchodytes meleagrinae* has been found in the cloaca of holothurians but this is a niche that has not been exhaustively examined for its inhabitants.

The Crinoidea, particularly the comatulids, are hosts for many shrimps. The genus *Palaemonella* Dana has one species found on several host crinoids, as are several species of *Periclimenes*. Other pontoniine genera found exclusively on crinoids are *Parapontonia* Bruce and *Pontoniopsis* Borradaile, both monospecific genera. The genus *Araiopontonia* Fujino and Miyake is probably also a crinoid associate. In the Alpheidae, several species of *Synalpheus* are crinoid commensals. No gnathophyllids or other shrimps have been found on crinoids.

Ascidians are hosts for a variety of pontoniine shrimps, species of *Pontonia* Latreille, and also *Dasella herdmaniae* Lebour. These, and also some species of *Synalpheus*, are found in simple ascidians. Some species of *Periclimenaeus* are to be found in cavities in compound ascidians.

Finally, some coral reef shrimps are associated with fishes. Two separate types of relationship are involved, one permanent and one transient. In the former, alpheid shrimps of the genus *Alpheus* share a burrow with a variety of small gobies. In the second type, the "cleaner" relationship is involved. Amongst the Indo-West Pacific Caridea only two shrimps appear to have been confirmed as cleaners of fish so far, the palaemonine *Leandrites cyltorhynchus* Fujino and Miyake and the hippolytid *Lysmata grabhami* (Gordon). Some species of the genus *Periclimenes* may possibly also act as cleaners.

Host Specificity

The problem of host specificity on these associations is of special interest. Some shrimps are completely restricted to a single host species. In contrast some others are very catholic in their selection of host. As an example of stenohospitic associations, the shrimps *Platycaris latirostris* Holthuis, *Ischnopontonia lophos* *Anapontonia denticauda* Bruce and *Racilius compressus* are all limited to the single coral host species *Galaxea fascicularis*. These shrimps all belong to highly specialized monospecific genera. *Thor amboinensis* is a euryhospitic shrimp which can be found in association with a wide variety of coelenterates including anemones, corals, alcyonarians and hydroids. In many cases in the Pontoniinae all the species of a genus are commensals, generally of the same group of animals; but exceptions do occur. In *Palaemonella*, a genus with five species, four are apparently free-living and one, *P. pottsi* (Borradaile), is associated with crinoids.

Similarly in *Thor*, with five species, two are associated with coelenterates, *T. spinosus* and *T. amboinensis*, and two of the three others are free-living amongst algae and sea grasses. In the alpheid genus *Athanas*, many species are free-living, but several

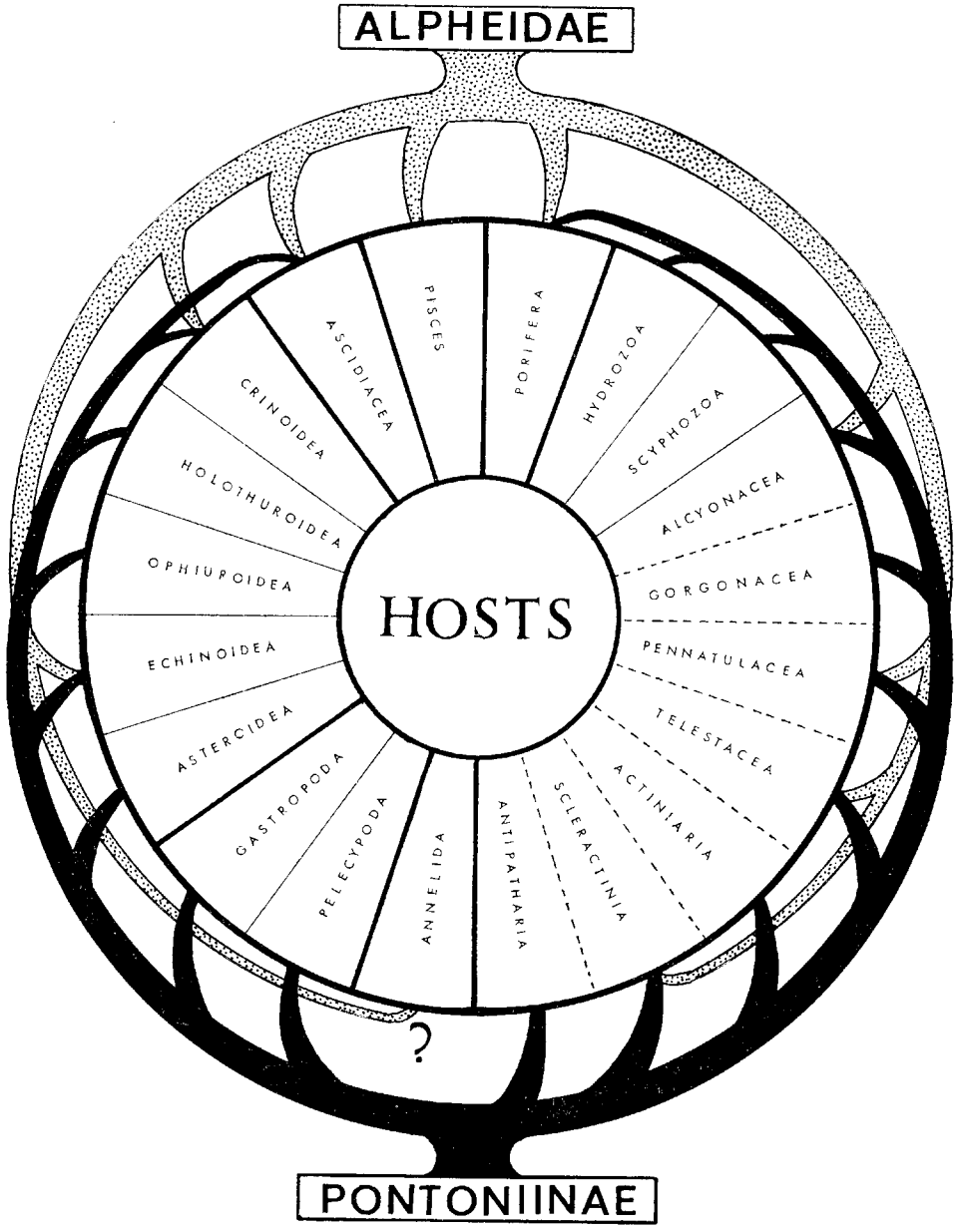

Fig. 2. A comparison of the range of host types involved in the associations of Indo-West Pacific shrimps in the family Alpheidae and the Subfamily Pontoniinae.

are associated with echinoids, and in *Alpheus*, most species are free-living, but others are found on corals, alcyonarians and also sponges and with fish. In *Synalpheus*, all species appear to be commensals but the precise niche of many species of this large genus remains to be established. The hosts for *Synalpheus* species cover a wider spectrum than any other alpheid genus and include sponges, corals, alcyonarians, pennatulaceans, telestaceans, crinoids and ascidians. At the species level, few shrimps have been found to associate with hosts of different phyla and most are not even able to cross barriers between hosts at the class level. The hippolytid *Hippolyte commensalis* is found on both hydroid and anthozoan hosts, as are also *Thor spinosus* and *T. amboinensis*. The shrimp *Periclimenes imperator*, which is generally found on nudibranch molluscs, is also frequently found on a variety of holothurians such as *Stichopus* and *Bohadschia* and also on synaptids such as *Opheodesoma*. This shrimp has also been photographed on an unidentified host by Valerie Taylor (Fig. 1) on Heron Island, on the Australian Great Barrier Reef. The host was swimming along about three feet below the water surface, with a squirming motion, and was quite firm and tough, not jelly-like, with a definite head end. It is presumably a large nudibranch also.

Adaptions

Many of these commensal shrimps have been much modified morphologically, especially in the Pontoniinae, which are associated with the widest variety of hosts (Fig. 2). In this group, the unspecialized body form is exhibited by free-living predatory species such as *Palaemonella rotumana* (Borradaile) or *Periclimenes grandis* (Stimpson). These contrast strongly with the greatly swollen shape of *Paratypton siebenrocki* which leads an incarcerated existence in coral cysts, or with the greatly elongated slender form of *Stegopontonia commensalis* Nobili, which clings to the slender spines of sea urchins. The adoption of a commensal way of life does not necessarily involve a marked degree of morphological change. For example, *Palaemonella pottsi*, a crinoid commensal, is morphologically almost indistinguishable from the free-living *P. rotumana*, and the two were for long considered synonymous. Some examples of morphological modifications of the body are well shown by the shrimps found in the narrow spaces between the corallites of *Galaxea fascicularis*. The alpheid *Racilius compressus* is very strongly bilaterally compressed. It was originally described as like a piece of paste board. As a result it can pass easily through the spaces between the corallites and is freely mobile. The pontoniine *Ischnopontonia lophos* is similarly compressed and also freely mobile. In contrast, *Platycaris latirostris* is strongly depresed and it is sedentary, clinging to a corallite in a head-down position. The two mobile species have well developed holdfast mechanisms in the caudal fans, as does also the smaller and less mobile, bilaterally compressed *Anapontonia denticanda*, but these are lacking from the *Platycaris*. Some of the shrimps that live in tubular cavities in sponges have tubular bodies to fit, often rather elongated and presenting a rather worm-like

appearance. In those species that live in confined spaces there is generally a tendancy towards the progressive reduction of the rostrum and loss of spines and other processes. The chelae show a bewildering range of variation, the significance of which is not apparent. Both alpheid and pontoniine shrimps have developed sound-producing mechanisms on the "pit and hammer" principle, although it is on the first pair of pereiopods in the Alpheidae and on the second pair in the Pontoniinae. In the genera *Alpheus* and *Synalpheus*, the mechanism involves small circular suction discs at the base of the dactylus and on the adjacent part of the chela, but these are not present in the pontoniine sound-producing genera such as *Coralliocaris* or *Periclimenaeus*. *Periclimenaeus* also resembles *Alpheus* in that only one chela is specialized for sound production, but in *Coralliocaris* these mechanisms may be developed on both sides of the body. The dactyls on the ends of the walking legs also show a great variety of modifications, with the development of extra teeth and hooks, which are presumably related to helping the shrimp cling to their particular host animal. Particularly well developed are these dactyls in the sponge- and tunicate-inhabiting species of *Periclimenaeus* and *Pontonia*.

In addition to morphological adaptions, many shrimps show adaptive colour patterns that are clearly related to their hosts. These are usually particularly well developed in those species that live in comparatively exposed situations, such as *Pontonides* sp. or *Dasycaris zanzibarica* on *Cirripathes*. Others also in exposed situations, such as *Propontonia pellucida* on *Sarcophyton* and other alcyonarians, may be completely transpasent. Many of the species that live in secure niches have bright colours that contrast strongly with their hosts. Examples of these are the coral-inhabiting alpheids *Alpheus lottini* and *Synalpheus charon* which are orange-red and scarlet respectively, and some species of pontoniine, such as the bright green *Coralliocaris graminea* and *C. viridis* or the white *C. superba*.

Many of the commensal shrimps are of very small size, an adaption to their particular niches. *Fennera chacei*, when fully grown, are only 5–6 mm long. Most of the commensal species are around 20 mm in length but some of the large *Alpheus* species are about 40 mm. The small size and cryptic habits make many of the shrimps very difficult to locate in their natural habitat. A few shrimps do stand out conspicuously against their backgrounds. One example is the hippolytid cleaner *Lysmata grabhami*. Other conspicuously coloured shrimps that contrast with their habitats are the species of *Rhynchocinetes*, but these seem to be active only at night, remaining well concealed in coral heads or in caves by day.

Life Histories

Very little is known about the life history and biology of these commensal shrimps. The larval stages of several pontoniine species from the Red Sea were reported upon by Gurney (1938) and the first larval stage of a number of other species have been subsequently described from hatchings. Almost all conform closely to type, but abbreviated development has been reported in *Pontonia minuta*,

the host of which is still unknown. The larvae of *Anchistioides* differ markedly from all other pontoniine larvae but the larvae of gnathophyllid shrimps (*Gnathophyllum* and *Hymenocera*) are very similar to those of the Pontoniinae. The larvae of many alpheid shrimps have also been described, some from coral reefs. Most species of *Alpheus* and *Synalpheus* hatch as normal Stage 1 larvae, but abbreviated development is more frequent than in the Pontoniinae, particularly in the genus *Synalpheus*. *Racilius compressus* also shows abbreviated larval development. The majority of coral reef carideans have a normal planktonic larval phase, after which they settle upon the reef substrate or, in the commensal species, upon their host animals. Probably many larvae from the latter never succeed in locating the appropriate hosts and so perish, but some species can probably prolong the early post-larval stage in which settlement occurs and become "pelagic bottom forms" (Wilson, 1952), as has been reported in the case of *Harpiliopsis depressus* (Bruce, 1970). These forms are probably important in the wide distribution of many species across the entire Indo-West Pacific even to the west American seaboard through "island-hopping."

Once settled upon their host animal, most commensal shrimps probably never leave it voluntarily. Some species are probably only associated with their hosts for shelter or protection from predators. These can feed independently and do not derive their sources of energy from the host. In this category one finds some alpheids of the genus *Athanas*, such as *A. indicus*, a common and widespread associate of the echinoid *Echinometra matthei*, and others. This species can easily be seen browsing on the substrate under the shelter of its host's spines under aquarium conditions. The pontoniines found on diadematid urchins, such as *Tuleariocaris* and *Stegopontonia*, are found only on the spines on the aboral surface of the host, where they have no access to the substrate; and these presumably feed either upon mucus derived from the host or on the plankton. Both species have well developed exopodites upon the three pairs of maxillipeds which are capable of forming a vortical current converging onto the anterior mouthparts. A similar mechanism is also present in some of the coral-inhabiting species, such as *Coralliocaris*; but in many others these exopodites are reduced or lacking and it seems likely that these feed upon the host in some unknown manner, possibly through the surface mucus with entrapped detritus.

Some of the most closely studied commensal shrimps are the pontoniines associated with bivalve molluscs, particularly *Anchistus custos*, which has been reported upon by Johnson and Liang (1966) in Singapore and from Madagascar by Jacquotte (1964), whose studies also included *Paranchistus ornatus* and *Conchodytes biunguculatus*, all of which occur in pinnid hosts. Johnson and Liang concluded that *A. custos* was a herbivore feeding upon algae taken from the feeding currents of the host, together with organic detritus and mucus.

Patton (1966) studied the commensal shrimp fauna of Queensland branching corals and clearly showed that a variety of species can be found in association with a single host colony, and the pontoniine associates of the various coral hosts have

also been reviewed by Bruce (1972). The coral associates are of particular interest on account of their variety. A single coral colony may provide a niche for a number of shrimp species, as well as crabs, galatheids, echinoderms, ascidians and fish. The interrelations of this fauna have not been investigated but presumably, in most cases, each species occupies its own niche in a manner that does not compete with the other species. In several cases there appear to be anomalous associations. The pontoniine shrimps *Jocaste lucina* and *J. japonica* may often be found together in mixed populations on the same host *Acropora.* These two shrimps form a species pair, with very minor morphological differences between them, and their colour patterns seem to be identical. Similarly, the three species of *Harpiliopsis* may be found together on a single *Stylophora* colony. *H. beaupresi* can be distinguished from the other two species by the details of its mouthparts, but the two other species can only be separated on the basis of morphological characteristics with some difficulty and are most readily identified in life by their characteristic colour patterns. If these two species feed upon the host mucus and associated detritus, it is not clear why competition does not eliminate one of them or how species identity can be manintained. If they feed on plankton, and well developed exopodites are present on the maxillipeds, then it is possible that some selection of foodstuffs does occur and competition between the two species of the pair can be avoided.

Multi-species associations are also often found in sponges, as well as on other coelenterates and on crinoids and echinoids, but in many other groups only a single male-female pair is to be found. This is the normal association in molluscs and ascidians. Juveniles may sometimes be found in association with these male-female pairs, and they may also be found occasionally on atypical host animals. For example, the juveniles of *Periclimenes brevicarpalis* have occasionally been found on alcyonarians instead of on anemones. These associations are probably the result of the settling post-larvae not being able to locate the appropriate host and being unable to delay settlement any longer. These juveniles generally seem unable to reach maturity and reproduce, and selection pressure is probably very high at this stage. If some do succeed, this would represent an important factor in the evolution of a further species of the genus. If a pair of individuals differ enough genetically from the original stock to survive and mature on the new host, it is to be expected that their progeny will be even more strongly adapted to the new host and the association will be reinforced.

The Incidence of Tropical Caridean Commensalism

The frequency of commensalism in the coral reef biotope is probably a most important contributory factor to the high species diversity found.

In a recent survey of the caridean fauna of the Kenyan National Marine Parks at Malindi, a total of 67 species of shrimp, with representatives of 7 families, was obtained. Although this number by no means represents the complete fauna, and many more species can be expected to occur, an analysis of the results shows

that of the species collected, only 29 were considered to be free-living and 38 species, 57 percent, were commensals. The collected fauna was dominated by the Pontoniinae, with 32 species representing 48 percent of the fauna, with the Alpheidae next in importance with 21 species (23 percent), followed by the Hippolytidae with 9 species. Four other families were represented by a single species only. In the species of the Pontoniinae (no specimens of the subfamily Palaemoninae were collected), 28 species out of the 32 collected are commensals, i.e., 88 percent. Similarly in the Alpheidae and Hippolytidae, the incidence of commensalism among the species represented in the collection is 24 percent and 44 percent respectively.

The range of host associations of these commensal species is also of interest. Of the 38 species, 20 (53 percent) were found in association with scleractinian corals. Next in importance, at a distinctly lower level, are the hydroid and echinoderm associates, each with four species or 11 percent. Both the sponges and the alcyonarians provide hosts for a further three species each, at 8 percent, and the Mollusca is host for only two species or 5 percent. A gorgonian and an anemone are also each host for a single shrimp species at 2.6 percent of the fauna.

A similar survey has been recently carried out on the fringing reefs of Mauritius and the results provide an essentially similar picture. About 80 species were collected, but some of the alpheid shrimps still remain to be fully identified. Of these 80 species, 49 percent are considered to be commensals. The fauna collected is again dominated by the Pontoniinae, with 37 species, of which 78 percent are commensals. The incidence in the Alpheidae is comparatively low, most species being apparently free-living burrowers, and only six (24 percent) are thought to be commensals. In the Hippolytidae, out of the nine species collected, 33 percent are commensals. Four species of the Palaemoninae were collected from Mauritius but only one of these, *Leandrites cyrtorhynchus*, a fish cleaner shrimp, is considered as a commensal.

The pontoniine fauna of the Seychelle Islands in the western Indian Ocean has been studied in some detail. At present 50 species are known, represented by 18 genera, all of which, except for one, contain some commensal species. Of these 50 species, 74 percent are known to be commensals, although as the trophic status of some species is still uncertain, the incidence of commensalism is probably silghtly higher. The distribution of host animals associated with these commensal species is as follows:

Coelenterata	62%	Scleractinea	54.0%
		Actiniaria	5.4%
		Alcyonacea	2.7%
Mollusca	16%	Pelecypoda	14.0%
		Gastropoda	2.0%
Echinodermata	11%	Echinoidea	5.4%
		Crinoidea	2.7%
		Asteroidea	2.7%
Porifera	11%		

Most of these species are of widespread distribution throughout the whole Indo-West Pacific region, although six are known only from the Seychelle Islands as yet.

The East African pontoniine fauna, principally from the regions of Zanzibar and Mombasa, has been studied over several years. At present 119 species have been found, a few of which are still undescribed. Thirty-five genera are represented, of which 18 are monospecific. Of these shrimps, 105 species are thought to be commensals, i.e., 88 percent. The incidence of commensalism in the family Alpheidae in this region is not known. The fauna of the Indonesian archipelago has been studied by the Siboga and Snellius Expeditions, and 69 species of pontoniine were reported upon (Holthuis, 1952). A total of 74 species are now known, of which 49, or 66 percent, are considered to be commensals. The Indonesian archipelago is often stated to be the region of highest species diversity for many groups of marine animals (Ekman, 1953); and it seems highly probable that more detailed study in that region would reveal the presence of many of the East African species, some of which extend into the Central Pacific Region. One of the most noticeable features of the shallow-water carideans is their wide and uniform distribution from East Africa and the Red Sea to Hawaii and Tahiti.

The Shallow Water Tropical Caridean Fauna

At the present time, some 210 genera of caridean shrimps are known. Of these, 98 are represented in the shallow-water tropical marine biotope. Amongst these genera, 62 percent are known to include some commensal species. This figure contrasts strongly with the overall incidence of commensalism in all caridean genera at 29 percent. The number of genera occurring in the tropical marine regions shows marked variations. Of the shallow-water caridean genera, 91 are found in the Indo-West Pacific region, which clearly indicates its faunistic richness when compared with the 41 genera that occur in the Atlantic region and the 28 genera found in the East Pacific region. The incidence of commensalism at generic level also shows marked variations in the three regions and is highest in the Indo-West Pacific, at 59 percent, compared with 50 percent in the East Pacific and only 41 percent in the Atlantic regions. The high figure for the Indo-West Pacific region is probably associated with the general extent of coral reef development in that region.

As mentioned above, the caridean fauna from the restricted area of the Kenyan Marine Parks is so far represented by 67 species, although a number of common East African species still remain to be collected there. The region studied is typical of many Indian Ocean reefs, and a similar fauna can be expected elsewhere in the region. From a restricted rocky shore in temperate waters such as around the British Isles, it would be unusual to find more than half a dozen shrimp species at one locality and amongst these the incidence of commensalism would be zero. Around the British Isles, commensalism amongst decapods is extremely rare and among the shrimps only a single example has been reported, *Typton spongicola* Costa, which is occasionally found in sponges off the southwest coast.

To indicate the richness of the tropical shallow marine fauna, the situation in East Africa, which is probably as rich as any locality, can be roughly assessed. From around Zanzibar and Mombasa, 119 pontoniines have so far been collected together with eight palaemonine species. As yet the alpheids have only been very incompletely studied and some 55 species identified. This number could probably easily be doubled by further investigation. Of the Hippolytidae, 20 species have been collected, and of the Processidae, 8 species. Nine other families are also represented by 5 species or less, totalling 22 species. A total caridean fauna of 232 species is now known. It is certain that many species must still remain to be discovered as some habitats, such as the reef front, are still almost completely unstudied since most collections have been made in the lagoons or other sheltered regions.

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