The Natantian Shrimps (Crustacea, Decapoda) Associated with Invertebrates in Hawaii¹

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NUMEROUS INSTANCES OF SYMBIOTIC ASSOCIATIONS between natantian shrimps and other invertebrates have been reported in the literature (see reviews by Balss, 1956 and Patton, 1967). These associations have generally been considered to be examples of commensalism on the basis that the host offers shelter to the smaller associate without being "harmed" by its presence. They are grouped here with other heterospecific associations (parasitism, mutualism, etc.) under the term symbiosis.

This checklist is a summary of general information on the natantian shrimps found associated with marine invertebrates in the Hawaiian Islands. It is based mostly on collections and observations made by the author. The checklist is intended not only as a guide for the quick identification of the shrimps but, hopefully, as an incentive for studies on the ecological, behavioral, and physiological aspects of the symbioses.

All synonyms and the most important references are given for each of the shrimp species. The diagnoses have been prepared by stressing those characters which can be easily observed in the specimens. Hosts listed are those recorded from Hawaii. Most hosts are common littoral forms and an examination of invertebrates from deeper water will probably result in the finding of new hosts and additional symbionts.

Fourteen species from three families of Natantia were found to be always in close association with other invertebrates. The groups serving as hosts and the number of associates in each is given as follows: Madreporaria (4), Echinoidea (4), Porifera (2), Antipatharia (1), Gastropoda (1), Pelecypoda (1), and Asteroidea (1).

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LIST OF SPECIES

FAMILY PALAEMONIDAE

All species listed under this family are members of the subfamily Pontoniinae. Holthuis (1955) has given a key to most of the genera.

Periclimenes soror Nobili

Periclimenes soror Nobili, 1904, p. 232; Kemp, 1922, p. 165; Gordon, 1939, p. 395, figs. 1–3 (redescription); Holthuis, 1952, pp. 9, 51, fig. 17, table (complete references)

Periclimenes bicolor Edmondson, 1935, p. 10, fig. 3

Hosts

Hosts are Acanthaster planci (Linn.), Culcita novaeguineae arenosa Perrier, Mithrodia bradleyi Verrill, and Linckia multifora (Lamarck) (Asteroidea).

Diagnosis

Rostrum is compressed and armed with 10 to 13 dorsal teeth; ventral border without teeth. Body is red, light yellow, or orange (sometimes with a white stripe on each side), depending on the color of the host.

Remarks

Individuals are normally found on the oral surface of the host, sometimes entering into the ambulacral grooves. One to 24 individuals have

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been observed in single starfish. Largest specimens reach a total length of 13 mm.

Recorded from several Indo-West-Pacific locations in association with various species of asteroids and one holothuroid (Bruce, 1965).

Periclimenes imperator Bruce

Periclimenes imperator Bruce, 1967, p. 53, figs. 23–25.

Hosts

Hosts are Hexabranchus aureomarginatus Ostergaard, Dendrodoris tuberculosa (Quoy and Gaimard) (Gastropoda, Nudibranchia, Dorioidea).

Diagnosis

Rostrum is compressed and conspicuously convex, its dorsal border armed with 23 to 30 small teeth; ventral border without teeth. Body is orange to red, with a broad white band across the carapace immediately behind the rostrum and another along the dorsal surface of the abdomen.

Remarks

Single pairs are occasionally found on the surface of nudibranchs. Largest specimens reach a total length of 20 mm.

Recorded associated with nudibranchs from the Indian Ocean and the Red Sea.

Onycocaris quadratophthalma (Balss)

Pontonia quadratophthalma Balss, 1921, p. 15, fig. 7; Edmondson, 1946, p. 250, fig. 150 c

Onycocaris quadratophthalma Holthuis, 1952, pp. 15, 150, table (complete references); Holthuis, 1955, fig. 36; Fujino and Miyake, 1969, p. 435, figs. 16–18

Host

Host is *Toxadocia violacea* de Laubenfels (Porifera, Demospongia).

Diagnosis

Rostrum is minute, not reaching beyond the eyes, and without teeth. First pair of pereiopods is very slender; second pair with enlarged and compressed chelae. Adult females have a conspicuously swollen body. Color is transparentwhite.

Remarks

Individuals are found in relative abundance inside the spongocoel of the host, a tubular sponge from shallow water. Largest specimens reach a total length of 14 mm.

The species is known from the Pacific Ocean and Northwestern Australia. Fujino and Miyake (1969) obtained specimens from "the base of branching corals" in the Ryukyu Islands.

Harpiliopsis depressus (Stimpson)

Harpilius depressus Stimpson, 1861, p. 38; Rathbun, 1906, p. 920, text fig, 68, pl. 24, fig. 12; Kemp, 1922, pp. 226, 228, 231, figs. 69, 70; Edmondson, 1946, p. 248, fig. 149

Anchistia spinigera Ortmann, 1890, p. 511, pl. 36, figs. 23, 23 a

Periclimenes spinigerus Borradaile, 1898, p. 1004

Harpiliopsis depressus Holthuis, 1951, p. 70, pls. 21, 22 (complete references); Holthuis, 1952, pp. 16, 182, fig. 90, table; Holthuis, 1955, fig. 40a

Hosts

Hosts are *Pocillopora meandrina* var. *nobilis* Verrill and *P. ligulata* Dana (Anthozoa, Madreporaria).

Diagnosis

Body is strongly depressed. Rostrum is compressed, its dorsal border armed with five to seven teeth and the ventral border with two to five teeth. Pleurae of the last two abdominal segments end in the form of acute teeth. Body almost transparent, with thin bluish stripes running along its dorsal surface.

Remarks

Individuals are commonly found on the branches of living *Pocillopora*, the number of shrimp in each colony depending on the size of the coral head. Barry (1965) analyzed the stomach contents of four individuals and found

coral mucus, zooxanthellae, and algal spores in two of them. Largest specimens reach a total length of 17 mm but females as long as 27 mm have been recorded (Holthuis, 1951).

The species is widely distributed throughout the Indo-West-Pacific region and the tropical eastern Pacific. It has been recorded from various species of the madreporarian corals *Pocillopora*, *Porites*, *Acropora*, *Seriatopora*, and *Stylophora*. Jacquotte (1964) found a pair between the spines of the echinoid *Echinometra mathaei* (de Blainville).

Conchodytes tridacnae Peters

Conchodytes tridacnae Peters, 1852, p. 594; Kemp, 1922, pp. 279, 283, fig. 105; Holthuis, 1952, pp. 17, 195, fig. 95, table (complete references); Miyake and Fujino, 1968, p. 426, fig. 8, table

Conchodytes meleagrinae Peters, 1852, p. 594; Edmondson, 1946, p. 250, fig. 151

Pontonia tridacnae Dana, 1852, p. 571, pl. 37, fig. 1

Pontonia meleagrinae Bate, 1888, p. 707, pl. 124, figs. 1, 2

Host

Host is Mollusca, Pelecypoda: Pinctada margaritifera (Linn.).

Diagnosis

Rostrum is depressed, curved downwards, and without teeth. Second pair of pereiopods are greatly enlarged. Body color is transparent-pink, with darker spots on the dorsal surface of the body and pereiopods.

Remarks

Single pairs have been found in the mantle cavity of the pearl oyster. Females may reach a total length of 30 mm.

The species is known throughout the Indo-West-Pacific region. It has been recorded from species of *Pinctada*, *Tridacna*, and *Pinna*, as well as from the cloaca of a holothurian (Chopra, 1931).

Stegopontonia commensalis Nobili

Stegopontonia commensalis Nobili, 1906, p. 258. Nobili, 1907, p. 360, pl. 1, fig. 2. Kemp, 1922, p. 268. Holthuis, 1952, p. 16, table. Holthuis, 1955, fig. 32a

Hosts

Hosts are Echinothrix calamaris (Pallas), E. diadema (Linn.), and Diadema paucispinum A. Agassiz (Echinoidea).

Diagnosis

Rostrum is broad, depressed (lanceolated in dorsal view), and with a longitudinal carina running along its ventral surface. Body is dark purple, almost black, with a thin white line running along each side.

Remarks

Single pairs of the shrimp are found living on the primary spines of the host. Not common. Largest specimens reach a total length of 35 mm.

Recorded associated with species of *Echinothrix* and *Diadema* from several Indo-Pacific locations.

Tuleariocaris holthuisi Hipeau-Jacquotte

Tuleariocaris holthuisi Hipeau-Jacquotte, 1965, p. 247, pls. 1–5; Bruce, 1967, p. 43

Hosts

Hosts are Echinothrix diadema (Linn.) and Astropyga radiata (Leske) (Echinoidea).

Diagnosis

Rostrum is compressed but provided with a supraocular midrib. Dorsal border is armed with six to eight teeth; ventral border without teeth. Three last pairs of pereiopods are composed of only six segments, the ischium and merus being fused. Individuals from *Echinothrix* are dark purple, almost black, changing to red at night; those from *Astropyga* are reddish-pink.

Remarks

Individuals are found living on the primary spines of the host, orienting the anterior end toward the base of the spines. Not common. Largest specimens reach a total length of 13 mm.

The species has also been recorded in association with the echinoids *Echinometra mathaei* (de Blainville) and *Stomopneustes variolaris* (Lamarck) from Madagascar (Hipeau-Jacquotte, 1965).

Pontonides sp.

Pontonia maldivensis Borradaile, 1915, p. 213

Pontonides maldivensis Borradaile, 1917, p. 387, pl. 57, fig. 28

?Pontonides uncinger Davis and Cohen, 1968, p. 749, figs. 1, 3

Host

Host is *Cirrhipathes* sp. (Anthozoa, Antipatharia).

Diagnosis

Body is depressed. Rostrum is compressed, slightly curved downward, and ending in a sharp point. It has a short and untoothed medial keel above and below. Yellow and greenish bands alternate across body.

Remarks

The only two specimens collected agree in most characters with Borradaile's description of *Pontonides maldivensis*. Nevertheless, his description is inadequate and the species needs redescription with a review of the genus (A. J. Bruce, personal communication). Hawaiian specimens collected by Davis and Cohen (1968) from the same host appear to represent the same species. This is also possibly true with the shrimp (referred to as *Pontonides* sp.) reported from *Antipathes grandis* Verrill by Grigg (1964).

The two individuals were observed between the polyps of the host, collected from a depth of 20 meters off Halona Blowhole, Oahu. *Pon*tonides maldivensis was described from an unspecified habitat in the Maldive Islands.

FAMILY GNATHOPHYLLIDAE

Members of this family can be easily recognized by their expanded, leaflike third maxilli-

peds. A key to the genera has been given by Holthuis (1955).

Gnathophylloides mammillatus (Edmondson)

Coralliocaris mammillata Edmondson, 1931, p. 5, pl. 1, fig. 2; Edmondson, 1946, p. 249

Host

Host is *Heterocentrotus mammillatus* (Linn.) (Echinoidea).

Diagnosis

Rostrum is very broad, depressed, and armed with four minute dorsal teeth. Second maxillipeds with an elongated, leglike endopod. Eyes sharply pointed. Body and appendages brick-red in color. Thin, dark lines are present along the dorsal surface of the body.

Remarks

Individuals are found clinging to the large primary spines of the host. At least one pair was found among all occupied sea urchins. The shrimp orient the anterior end toward the tip of the spines. Females may reach a total length of 15 mm. Shorter and stouter individuals have been observed between the flat secondary spines.

The species is known only from the Hawaiian Islands.

Gnathophylloides mineri Schmitt

Gnathophylloides mineri Schmitt, 1933, p. 7, fig. 3; Holthuis, 1955, fig. 52; Lewis, 1956, p. 288, figs. 1, 2

Hosts

Hosts are *Pseudoboletia indiana* (Michelin) and *Tripneustes gratilla* (Linn.) (Echinoidea).

Diagnosis

Rostrum is short, compressed, and armed with three to four dorsal teeth and a minute ventral tooth near the tip. Second maxillipeds with an endopod not longer than the exopod. Eyes are stout but not sharply pointed. Dorsal surface of the body is pink with thin and dark longitudinal lines. A broad, white band runs along each side of the carapace and abdomen; its inferior border is whitish (as in individuals found on *Tripneustes gratilla* or on white *Pseudoboletia indiana*) or purple on *P. indiana* with purple spines).

Remarks

Species is commonly found on the spines of the oral surface *P. indiana*. Rare on *Tripneustes gratilla*. As on *Heterocentrotus mammillatus*, individuals orient their anterior end to the tip of the sea urchin's spines. Maximum length recorded is 8 mm.

This is the first time the species is reported from the Indo-Pacific region. Schmitt (1933) described it from specimens collected from "coral reefs" in Puerto Rico. It has also been recorded associated with the echinoids *Tripneustes ventricosus* (Lamarck) and *Lytechinus variegatus* (Lamarck) from the Caribbean Sea and Florida (Lewis, 1956).

FAMILY ALPHEIDAE

In addition to the four species listed below, two alpheids have been recorded as apparent associates of invertebrates. Salmoneus mauiensis (Edmondson) was observed by Edmondson (1946) as being usually associated with a large polychaete (Eurythoe sp.). The shrimp, however, has apparently never been found again. Some specimens of Alpheus paradentipes Coutière have been collected from sponges (Banner, 1953).

Keys to most of the Hawaiian alpheids have been given by Banner (1953).

Synalpheus charon (Heller)

Alpheus charon Heller, 1861, p. 272, pl. 3, figs. 21, 22

Synalpheus charon Coutière, 1899, p. 264, figs. 331, 332; Banner, 1953, p. 37, fig. 11; Patton, 1966, p. 281, table I; Banner and Banner, 1967, p. 262

Synalpheus charon charon Banner, 1956, p. 331

Synalpheus charon obscurus Banner, 1956, p. 329, fig. 5

Synalpheus helleri de Man, 1911, p. 246, pl. 8, fig. 37

Hosts

Hosts are *Pocillopora meandrina* var. *nobilis* Verrill, *P. ligulata* Dana, and *P. cespitosa* Dana (Anthozoa, Madreporaria).

Diagnosis

Inferior hook of dactylus of third pereiopods has an expanded base, a spoonlike depression on inferior margin, and a broad, blunt tip. Superior hook is slightly longer and acute. Body is dark orange-red.

Remarks

Shrimps are very common in crevices at the base of living colonies of *P. meandrina* and *P. ligulata*. One pair is usually found in each colony. Individuals may reach a total length of 20 mm.

The species is known from several locations across the Indo-West-Pacific region and the Gulf of California. It appears to be an obligate associate of corals, especially of *Pocillopora*. Patton (1966) recorded it from the coral, *Stylophora*.

Synalpheus streptodactylus streptodactylus Coutière

Synalpheus neomeris streptodactylus Coutière, 1905, p. 870, pl. 70, fig. 1

Synalpheus streptodactylus de Man, 1911, p. 226, pl. 7, fig. 29

Synalpheus metaneomeris streptodactylus Coutière, 1921, p. 414, pl. 60, fig. 4

Synalpheus streptodactylus streptodactylus Banner and Banner, 1966 a, p. 157; Banner and Banner, 1966 b, p. 50, fig. 14, table I

Host

Host is Zygomycale parishii (Bowerbank) (Porifera, Demospongia).

Diagnosis

Inferior hook of dactylus of third pereiopods has base twice the diameter of superior hook, almost equal in length, and has an acute tip. Inferior margin of merus of third pereiopods armed with two to five movable spinules near its middle portion. Body is tannish-brown in color (D. M. Banner, personal communication).

Remarks

In Hawaii the species has been reported as occurring in abundant numbers in the spongocoel of *Z. parishii*, a large sponge (Banner and Banner, 1966 a). This appears not to be the case in the other locations of the Pacific and Indian Oceans where the species has been recorded. Barry (1965) collected it from dead coral in Hawaii.

Alpheus lottini Guérin

Alpheus lottini Guérin-Méneville, 1830, p. 38, pl. 3, fig. 3; Banner and Banner, 1964, p. 88 (notes on nomenclature); Banner and Banner, 1966 b, p. 91, fig. 31, table I

Alpheus ventrosus H. Milne Edwards, 1837, p. 352; Banner, 1958, p. 164, fig. 4; Patton, 1966, p. 282, tables I–III

Alpheus laevis Randall, 1839, p. 141

Alpheoides laevis Paulson, 1875, p. 106, pl. 14, fig. 3

Crangon laevis Urita, 1921, p. 217

Crangon ventrosus Edmondson, 1923, p. 29; Edmondson, 1946, p. 255, fig. 155

Crangon ventrosa Banner, 1953, p. 88, fig. 28 Crangon latipes Banner, 1953, p. 82, fig. 27

Hosts

Hosts are Anthozoa, Madreporaria: Pocillopora menadrina var. nobilis Verrill, P. ligulata Dana, and P. cespitosa Dana.

Diagnosis

Carina of rostrum is separated from orbital hoods by deep, narrow grooves. Dactylus of third pereiopods is blunt and compressed, with a longitudinal ridge on the inner side and a hooflike ridge on the tip. Body bright orangered, darker on dorsal surface (usually in the form of stripes or spots).

Remarks

Species is a common and conspicuous associate of *Pocillopora*. It is found in pairs in the spaces between the coral branches. Barry (1965)

found that the shrimp feed mostly on small invertebrates and algae from the coral branches, but that coral mucus and tissue are also ingested. Maximum total length recorded is approximately 40 mm.

The species is an apparent obligate associate of corals throughout its wide range. It is known from across the entire Indo-West-Pacific region and from the Gulf of California to the Galápagos Islands. It has been recorded from *Pocillopora*, *Seriatopora*, and *Stylophora*.

Alpheus deuteropus Hilgendorf

Alpheus deuteropus Hilgendorf, 1878, p. 834, pl. 4, figs. 8–10; Banner and Banner, 1964, p. 88; Banner and Banner, 1966b, p. 80, fig. 26, table I

Crangon deuteropus Banner, 1953, p. 70, fig. 22

Host

Host is *Porites lobata* Dana (Anthozoa, Madreporaria).

Diagnosis

Large and small chelae have dense hair along the inner surface. Merus of third pereiopods has a strong tooth on distal inferior border; dactylus is simple. Body is mostly transparent; carapace has sparsely scattered red chromatophores (D. M. Banner, personal communication).

Remarks

Single pairs are found living inside fissures on the surface of living coral colonies. The branching fissures are usually lined with short filamentous algae.

The species is known from locations across the Indo-West-Pacific region. It has been recorded from fissures on *Porites, Acropora*, and *Astreopora*.

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