Brachyuran Crabs Symbiotic with Scleractinian Corals: A Review of their Biology[1]

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INTRODUCTION

The brachyuran crabs constitute one of the most diverse components of coral reef communities. Serène (1972) has estimated that more than 500 of approximately 2,000 species of Indo-West Pacific brachyurans are inhabitants of coral reefs. Many of these species are associated in one way or another with scleractinian corals. Some of these are found living on dead coral or coral rubble while others are facultative or obligate associates of living coral.

This review will be limited to those brachyurans which are obligate associates of living scleractinian corals. Various terms have been used in designating these as well as other associates: "commensals," "parasites," "epizoics," "epibiotes," or simply "associates." Often these organisms are placed in a category after making assumptions on the presence or absence of "harm" or "benefit" in the partners. Here they will be referred to as "symbionts" following the original definition of symbiosis as different species living together (de Bary, 1879; see also Hertig *et al.*, 1937). Brachyurans which are normally restricted to live corals are therefore considered obligate symbionts. Facultative symbionts utilize live corals only as an alternate and often temporary habitat.

Symbiosis may be best visualized as a broad category of heterospecific associations involving a wide range of adaptive interactions. Differences between some symbiotic and predatory interactions have been outlined by Noble and Noble (1971). The criteria of harmfulness and of metabolic dependency (see Smyth, 1962; Cheng, 1967) have often been used in classifying symbioses. Such criteria, however, are difficult to apply to most brachyuran-coral symbioses due to our inadequate knowledge of their biology.

The distribution of brachyurans among dead and living corals has been investigated by Garth (1964). Serène (1972) has reviewed the brachyurans associated with coral reefs in general, but emphasis was given to some of the symbionts of scleractinian corals. Some of these symbioses are included in reviews of crustacean symbionts (Balss, 1956; Patton, 1967a), in a review of the predators and symbionts of stony corals (Robertson, 1970), and in several general reviews of symbiotic as-

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sociations (Caullery, 1952; Dales, 1957; Dales, 1966; Nicol, 1967; Gotto, 1969).

Brachyurans which are obligate symbionts of scleractinian corals belong to two families, Xanthidae and Hapalocarcinidae. Several xanthids, portunids, and a dromiid have been reported as symbionts of octocorals (see Balss, 1956; Patton, 1967a; Serène, 1972).

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XANTHIDAE

Most coral associates of all types are found included in this large family. *Trapezia* and *Tetralia*, common obligate symbionts, are generally grouped as a separate subfamily, the Trapeziinae. Other obligate and facultative symbionts are found among the other xanthid groups.

Trapezia

All species of *Trapezia* are obligate symbionts of scleractinian corals. A total of 23 species are included in a provisional key given by Serène (1969). The specific status of several color forms, however, is still questionable. The genus is widely distributed throughout the Indo-West Pacific region. Two species are found in the Eastern Pacific from the Gulf of California to Ecuador and the Galápagos Islands. Coral symbionts are some of the few species of decapod crustaceans to be present on both sides of the Pacific Ocean (see Garth, 1974a).

Branching pocilloporid corals belonging to three genera (*Pocillopora, Stylophora,* and *Seriatopora*) are the hosts of *Trapezia* throughout its range. Patton (1966) and Garth (1974b) have reported the presence of crabs on *Acropora*. Tests with adult crabs suggest a preference for *Pocillopora* over *Acropora* (Knudsen, 1967). Host specificity among the many pocilloporid species has not been analyzed.

The spatial distribution of crabs in their host has been studied by Barry (1965) and Preston (1973) in *Pocillopora meandrina* Verrill from Hawaii, and by Patton (1974) in *P. damicornis* (Linnaeus) from Australia. Mature crabs are typically found in heterosexual pairs. Paired individuals are usually very similar in size (see Preston, 1973; Patton, 1974). In most coral colonies only one pair is present per species but additional pairs may be found in the largest colonies. The mean species diversity of *Trapezia* and other decapod associates of *Pocillopora* generally increases with the size of the colony (Patton, 1974). Different color forms of morphologicallysimilar species have been observed by Patton to be always in pairs, an indication that they may represent distinct species (see also Garth, 1974b). Most pairs are found on the central branches with their anterior end pointed outwards. Smaller crabs (mature as well as juveniles) are more common at the base of the colony.

The establishment of territories is a consequence of pairing. Preston (1973) has suggested that territoriality is not only the result of competition for shelter but a way of minimizing intraspecific agonistic interaction between crabs. Host-size requirements for the five Hawaiian species studied by Preston were demonstrated to be statistically different.

Field and laboratory observations in the Hawaiian species have shown that crabs are capable of leaving coral colonies and exchanging hosts (Preston, 1971). The size difference between paired individuals was decreased as a result. Host-exchange behavior has been studied in a species of *Trapezia* from Panamá (Castro, unpublished). It was found that almost all of the movements outside the coral took place during the night.

Preston (1973) has made a detailed study of competition during host selection by adult crabs. A stochastic computer model was developed and used in simulation experiments of competition among five species. Results indicated that interference competition resulting from random encounters during host selection may explain the distribution patterns observed in the species.

The feeding habits of *Trapezia* have been mostly investigated by the analysis of stomach contents. "Worms" were found in the stomachs of two species collected from the Gulf of California (Crane, 1937). In the Hawaiian species Barry (1965) found material apparently obtained directly from the coral host (zooxanthellae, nematocysts, mucus) as well as coral fragments, small crustaceans, sponge spicules, and mollusc radulae. Stained coral tissue was readily ingested by starved crabs. It was concluded that although coral tissue and mucus appeared to have been ingested, food caught on the surface of the coral was more important. *Trapezia* and the other crustacean associates of corals were considered as detritus feeders and predators by Gerlach (1960). Knudsen (1967) observed that coral mucus was ingested by two species of *Trapezia* at Enewetak (Eniwetok). The feeding behavior of the crabs was also studied by Knudsen. Starved individuals were observed to scratch the coral surface with their walking legs, after which the tips were cleaned by the mouthparts. The dactylus of each walking leg was found to be provided with short and stout spines at the distal end ("food brush") and a dense tuft of feathered bristles on the ventral border ("food comb"). The food brush was suggested to be used in shaking coral polyps and the food comb to collect and concentrate mucus, bacteria, and debris. The chelipeds were observed not to be used actively in feeding. While most authors have referred to *Trapezia* as a "commensal," Knudsen considered it an "obligate ectoparasite" since material from live coral is used as food. A feeding behavior similar to that described by Knudsen has been observed by Patton (1974) and by this author. Preston (1973) examined the stomach contents of the five Hawaiian species. Mucus was the predominant material but sponge spicules and sand grains were also common. The latter were given as evidence that feeding may take place at the dead coral base. Patton (1974) analyzed the stomach contents of three species by using Toluidine blue as a way of demonstrating the presence of mucus (see Goreau, 1956). Crabs were found to feed on coral mucus as well as particulate organic matter (organic aggregates) settling on the coral. Fragments of sponge spicules, forminiferans, mineral particles, bacteria, and other types of debris were observed. It was suggested that *Trapezia* and the other symbiotic decapods ingest the abundant mucus which is secreted by the coral as a way of extruding particulate material from its surface. This may explain the many types of particulate material recorded from the stomach of *Trapezia* and other coral symbionts.

There are few reported cases of predation on *Trapezia*. Remains of crabs have been found in the stomach contents of several fish (Hiatt and Strasburg, 1960) and a sea star, *Leiaster leachi* (Gray) (Garth, 1973). Remains have also been found around the entrance of shelters inhabited by octopuses (Castro, unpublished). Predation may be more effective during the movement of the uncamouflaged crabs outside the host. Fish which are predators of corals or those which break into coral colonies may also be important (see Glynn *et al.*, 1972). The role of *Trapezia* in defending the coral from a predatory sea star, *Acanthaster planci* (Linnaeus), has been suggested from several observations (Pearson and Endean, 1969; Weber and Woodhead, 1970; Glynn, unpublished).

The complete larval development of *Trapezia* is unknown. The first zoeal stage has been described in three species, two by Gurney (1938) and one by Al-Kholy (1963b). Knudsen (1967) observed that the first zoea of *Trapezia* showed a positive chemotactic response.

Tetralia

Tetralia may be best described as the analogue of *Trapezia* in acroporid corals. Two species (*T. glaberrima* (Herbst) and *T. heterodactyla* Heller) are generally recognized but several color forms have been described (see Serène and Dat, 1957; Patton, 1966). The genus is apparently restricted to the many species of *Acropora* found throughout the Indo-West Pacific region, although Garth (1964) reported the finding of a few individuals on *Seriatopora* and *Pocillopora*, two pocilloporid genera. Preference for *Acropora* over *Pocillopora* is suggested by tests made by Knudsen (1967).

Crabs are found living in pairs, usually one pair per coral colony (Garth, 1964; Garth, 1974b). In the species of *Acropora* with large, plate-like colonies, Garth (1964) found numerous crabs, a total of 27 males and 16 females in one instance. The smallest form of *Tetralia* was found on the plate-like corals, whereas the larger forms were found on the more robust, clump-like corals. The existence of territoriality and the factors affecting the distribution of crabs on the coral colonies have not been investigated.

Knudsen (1967) presents evidence that suggests that *Tetralia*, like *Trapezia*, ingests coral mucus and its associated detritus. The walking legs were found to be somewhat similar to those of *Trapezia*. The dactyli are provided with small terminal setae ("food brushes") and two rows of blunt, unfeathered bristles ("food comb") along the ventral surface. The preference of *Tetralia* for species of *Acropora* (in contrast to that of *Trapezia* for pocilloporid corals) is suggested by Knudsen as being related to the relative size and the efficiency of the food brushes and combs in both genera. *Tetralia*, with its smaller feeding apparatus, was seen as taking advantage of the larger amounts of mucus observed to be characteristic of *Acropora*. *Tetralia* is considered by Knudsen as an "obligate ectoparasite" of corals.

Only part of the larval development of *Tetralia* is known. Al-Kholy (1963a) has described three zoeal stages of *T. glaberrima*. The first zoea of the same species was described by Gurney (1938). Frontier (1963) described a first zoea and an advanced zoea attributed to *Tetralia*. As in *Trapezia*, the first zoea was observed by Knudsen (1967) to show a positive phototactic response.

Domecia

The three species in this circumtropical genus are symbionts of scleractinian corals. Two species, *D. hispida* Eydoux & Souleyet and *D. glabra* Alcock, are widely distributed in the Indo-West Pacific region. *D. hispida*, also found in the tropical Eastern Pacific, appears to be restricted to pocilloporid corals (Barry, 1965; Garth, 1964; Patton, 1966; Garth, 1974b) while *D. glabra* has been found on various species of *Acropora* (Garth, 1964; Patton, 1966; Garth, 1974b). In some of the earlier reports *D. hispida* is recorded from "sponges and branches of corals and in holes of dead corals and stones" (Rathbun, 1930), "algal masses" (Holthuis, 1953), or dredged from locations where live coral was not recorded (Garth, 1946). Nevertheless, its presence in the Eastern Pacific together with other decapod symbionts of *Pocillopora* (in contrast to the absence there of *D. glabra* and its *Acropora* hosts) is an indication of the possible obligate nature of the association. A third species, *D. acanthophora* (Desbonne & Schramm), is present on both sides of the tropical Atlantic. It has been recorded from *Acropora, Porites,* and *Meandrina* in the Caribbean Sea (Rathbun, 1930; Patton, 1967b) and from unidentified corals in several locations along the African coast (Guinot, 1964).

Patton (1967b) has studied various aspects of the biology of *D. acanthophora* in Puerto Rico. Crabs were found inhabiting shallow crevices, pits, and modified spaces between vertical branches in its most common host, *Acropora palmata* (Lamarck), a coral characterized by large, plate-like branches. Patton suggests that these "resting places" result as a response of the coral to the physical contact of crabs. There was no evidence of heterosexual pairing or territoriality. Empty resting places were occupied by crabs apparently moving from other coral colonies. Resting places were not observed in two branching species of *Acropora*. From the analysis of stomach contents and the examination of mouthparts Patton concluded that organic detritus removed from the water was the most important source of nutrition. Coral mucus was suggested as a possible but less important food. Most of the material found in the stomach of 14 individuals was a "white, structureless mass containing various amounts of large bacteria." The mouthparts and stomach contents of a specimen of *D. hispida* from the Galápagos Islands were found to be very similar to those of *D. acanthophora*. Crane (1937) found "indeterminate organic matter" in the stomachs of specimens of *D. hispida* from the Gulf of California. Barry (1965) observed the remains of "small crustaceans" in the stomach contents of the same species in Hawaii.

D. hispida has been observed living in pairs between the branches at the base of *Pocillopora* (Barry, 1965). Pairing has also been reported by Garth (1974b). The two Indo-Pacific species apparently do not induce any structural modifications in the host.

Cymo

All four species of *Cymo* are known to be associated with living scleractinian corals. *C. deplanatus* H. Milne Edwards and *C. melanodactylus* Dana are apparently restricted to species of *Acropora*, while *C. andreossyi* (Audouin) and *C. quadrilobatus* Miers have been recorded mostly from pocilloporid corals and occasionally from dead coral (Garth, 1964; Patton, 1966; Patton, 1974; Garth, 1974b). Johnson (1962) has suggested that (in at least two species) "the reduced eyes and the very large abdomen under which the females carries many eggs are striking features paralleling. . .the Hapalocarcinidae," a group of highly specialized coral symbionts. Patton (1974), however, considered *C. andreossyi* to be in a group of symbionts that show "slight morphological differences from typical free-living species."

Johnson (1962) has reported two species of *Cymo* as "inhabitating crypts of foliaceous living corals" in Singapore. Such structures were not observed by Patton (1974) in *C. andreossyi* from Australia. This species was infrequently found in pairs although one to three individuals were present in inhabited coral colonies. From the analysis of stomach contents (mineral fragments, "soft material with inclusions of small particles," and sponge spicules) Patton suggests that sediment and coral mucus are the most probable food. Most individuals of two of the three species of *Cymo* collected by Garth (1974b) were present in heterosexual pairs. Crabs were observed to inhabit burrows in the base of the coral.

The first zoea of *C. andreossyi* has been described by Gurney (1938). No other larval stages are known.

Maldivia

Very little is known about the biology of *Maldivia*. Four species are usually recognized, three of which are known from various locations in the Indo-West Pacific and one from the tropical Eastern Pacific. There is only scant information on the habitat of these species. *M. symbiotica* Borradaile has been collected from a gorgonian in the Maldive Islands (Borradaile, 1902). *M. triunguiculata* (Borradaile) is known from two scleractinian corals in the Indian Ocean: *Leptoria* (Borradaile, 1902) and *Galaxea* (Garth, 1974a). The species is listed by Borradaile as *Pseudozius triunguiculatus* Borradaile (Garth, 1969). *M. galapagensis* Garth, the Eastern Pacific species, was recovered from water in which a coral (an unidentified species of *Pavona*) had been rinsed (Garth, 1939; Garth, 1946).

Facultative Symbionts

A considerable number of xanthid species have been reported from live as well as from dead coral or other habitats. Many of these records are perhaps the result of the sporadic movement of crabs into live coral or to inadequate sampling procedures. It has been observed that crabs are likely to move into the live portion of a coral colony even when it is carefully segregated from the dead base at the time of collection. In many cases, especially in the earlier literature, inadequate or ambiguous information is given for the habitats. As Serène (1972) has pointed out, "the traditional indication 'coral reef' on the label of the brachyuran specimens strongly needs to be improved." Several species, however, have been repeatedly collected as occasional inhabitants of live coral.

Actaea speciosa (Dana) has been considered by Barry (1965) as an obligate inhabitant of live *Pocillopora* in Hawaii. Coral fragments and mucus were found to be ingested. Borradaile (1902) had observed a "brush of hairs" at the distal end of the first walking leg of this species, a feature which suggests a mucus-gathering structure similar to that described by Knudsen (1967) in *Trapezia*. *A. speciosa* has also been collected from live *Pocillopora* in the Maldive Islands (Garth, 1974b). Garth suggests that it should be considered a facultative symbiont since it occurred as solitary individuals rather than in heterosexual pairs.

Patton (1974) found *Chlorodiella nigra* (Forskal) and *Phymodius ungulatus* (H. Milne Edwards) commonly associated with live *Pocillopora* in Australia. Both species were suggested to be sediment-feeding or omnivorous forms also able to feed on coral mucus and its associated detritus. Other common facultative symbionts are *Liomera* (=*Carpilodes*) *cinctimana* (White), an Indo-Pacific species which together with many obligate symbionts is also present in the tropical Eastern Pacific (Garth, 1974a), and *Pilodius areolatus* (H. Milne Edwards). Additional species are listed by Garth (1964; 1974b).

HAPALOCARCINIDAE

All members of the Hapalocarcinidae are obligate symbionts of scleractinian corals. Hapalocarcinids are easily distinguished from other brachyurans by their small size and by their occurrence (with the exception of the males of some species) in galls or various types of cavities in the coral host. A monograph of the family by Fize and Serène (1957) gives abundant information on the geographical distribution and ecology of the known species. A subsequent partial revision by Serène (1967) recognizes a total of eight genera and 27 species. Most of the species are found only in the Indo-West Pacific region. Two are also present in the tropical Eastern Pacific and two are restricted to the tropical Atlantic. Careful examination of tropical stony corals will probably reveal new species.

Hapalocarcinus

Hapalocarcinus marsupialis Stimpson, the only species in the genus, is the best known hapalocarcinid. It has been recorded throughout the Indo-West Pacific and the Eastern Pacific inhabiting galls in branching pocilloporid corals of three genera, *Pocillopora, Stylophora,* and *Seriatopora* (see Fize and Serène, 1957). A record from a hydrocoral (*Millepora*) collected in the West Indies is the result of a misidentification (see Calman, 1899).

In *Hapalocarcinus* the females inhabit round to oval galls formed in the branches of the host. The stages in the development of galls in various corals have been described by Potts (1915) and Hiro (1937). Both concluded that galls are formed as a result of a modification in the growth of the coral. This process was explained as being triggered by the physical contact of a postlarval crab which had settled at the apex of a growing branch. A narrow crevice is first formed as the coral grows around the minute crab. According to Potts and Hiro, the constant, fixed respiratory currents of the crab laterally increase the outward growth of the branches thus giving shape to the gall. The expanded branches (plus neighboring branches in the case of corals with very slender branches) eventually meet, but a series of small apertures (referred to as "respiratory apertures" by Potts) remain along the outer border. The irregular shape shown by the coral polyps inside the gall was explained by Potts as being the result of the respiratory currents of the crab. Solitary mature females inhabit the main chamber of the gall (which can be up to 35 mm wide) while immature females are found in the original crevice in open galls. Mature females are characterized by a greatly expanded abdomen invariably containing hundreds of eggs. Closed galls were observed by Potts and Hiro to contain a dead female.

The male was first described by Potts (1915) from a single individual. It was subsequently studied by Fize (1956) and MacNamee (1961). Before its discovery, it was believed that copulation took place during a free living existence (Calman, 1899). Fize (1956) observed that the tiny males (carapace length of about 1.0 mm) show a close resemblance to the megalopa. Males were found inhabiting small shelters ("loges") formed at the junction of growing coral branches. Very little is known about its biology. Potts (1915) suggested that males are short lived and that copulation takes place while the galls are still open.

There is only scant information on the nutrition of *Hapalocarcinus* and the other hapalocarcinids. After studying the structure of the mouthparts and stomach (as well as the contents of one stomach), Potts (1915) assumed that females feed on the "nannoplankton" that enters into the galls with the respiratory currents. There is a reduction in some of the features of several mouthparts and the stomach, but the third maxillipeds are provided with numerous setae which characterize filter feeding brachyurans.

The complete larval development of *H. marsupialis* is unknown. The first zoea has been described by Potts (1915), Edmondson (1933), Fize (1956), and Al-Kholy (1963b); the megalopa by Fize (1956). The hatching zoeas probably leave the gall through the small apertures.

Other Genera

The remaining seven genera and 26 species of hapalocarcinids known at the present time inhabit various types of cavities or pits formed in the coral. The only exception is *Pseudohapalocarcinus ransoni* Fize & Serène, which forms partially opened galls in a species of *Pavona* (Fize and Serène, 1957). The external opening of the small cavities can be round, oval, or crescentic, depending on the species.

They can easily be mistaken with the cavities made by some barnacles, pelecypods, polychaetes, and other burrowing forms.

Most hapalocarcinids show a narrow host specificity. Almost all species are restricted to one or two genera of scleractinian corals. Corals belonging to a total of ten families serve as hosts (see Fize and Serène, 1957; Serène, 1972). Almost half of the total number of species are found exclusively in corals belonging to the family Faviidae.

The work of Potts (1915) and Hiro (1937) with *Cryptochirus* contains most of the scant information available on the biology of hapalocarcinids other than *Hapalocarcinus*. *Cryptochirus* typically forms cylindrical cavities in massive corals. The process involved in the formation of cavities has been assumed to start when a postlarval crab settles on a polyp. The polyp will eventually die, but the coral continues to grow around the theca, thus forming a cylindrical cavity around the crab. Females are always found in these cavities, which have been reported to reach 11.3 cm in depth (Hiro, 1937). The cephalothorax is almost cylindrical in cross section, but its anterior portion is obliquely flattened. The dorsal portion of the carapace is usually very colorful and provided with numerous bristles (see Fize and Serène, 1957). The crabs fit tightly in their cavities so that the anterior part of the carapace closes most of the opening much like the operculum of other coral tube-dwellers such as polychaetes and vermetid gastropods. A similar phenomenon has been observed in other hapalocarcinids. Crabs use their well-developed legs to hold to the sides of the cavity just below the opening. The walking legs and the cephalothorax are well adapted to close the opening in those species inhabiting crescentic cavities (see Utinomi, 1944; Garth, 1965; Garth and Hopkins, 1968). Hiro (1937) suggested that, at least in *Cryptochirus*, females move to larger cavities or start new ones after molting. This behavior may explain the wide variation observed in the depth of cavities.

The adult males are smaller than the females in most species. They typically inhabit similar but smaller cavities. The tiny males of *Cryptochirus dimorphus* Henderson were described as living together with females (Henderson, 1906). Edmondson (1933) described three species in which the males were found free-living. Potts (1915) believed that fertilization takes place when the solitary females come out of their cavities to molt.

Nothing is known about the feeding habits of these hapalocarcinids. The structure of the mouthparts, like those of *Hapalocarcinus*, indicates an adaptation for filter-feeding.

There is little information on the larval development of hapalocarcinids other than *Hapalocarcinus*. Edmondson (1933) described the first zoea of *Favicola* (= *Cryptochirus*) *minutus* (Edmondson), and Fize (1956) the first zoea and megalopa of *Pseudohapalocarcinus ransoni*.

SUGGESTIONS FOR FURTHER STUDY

The study of the symbioses between brachyurans and scleractinian corals presents a number of challenging problems. The questions are many and the possibilities almost endless. These include (1) interspecific and intraspecific interactions and space relationships in the host; (2) feeding habits, energetics, and nutritional physiology; (3) apparent immunity against coral nematocysts; (4) possible effect of symbionts on the growth of corals; (5) formation of galls and cavities by hapalocarcinids, especially the possible effect on coral calcification; (6) larval development and host selection.

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ADDENDUM

The crustaceans and other animals associated with reef corals have been recently reviewed by Patton (1976):

Patton, W. K. 1976. Animal associates of living reef corals. *In* O.A. Jones and R. Endean (eds.), Biology and Geology of Coral Reefs, Vol. 3, Biology 2.