6. Brachyuran decapod crustaceans of coral reef communities of the Seychelles and Amirante Islands

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Introduction

Following his participation in *Te Vega* Cruise B to the Maldive Islands, South India, and Ceylon, as a member of the U.S. Program in Biology of the International Indian Ocean Expedition, during which decapod crustaceans inhabiting hermatypic or reef-building corals were studied, the writer was deluged with collections from other western Indian Ocean localities, including Kenya, Somalia, and the Red Sea. Of them none has proved more rewarding than a collection from corals made in the Seychelles and Amirante Islands in 1966 by A.J. Bruce, which are the subject of the report that follows. The excellence of this collection consists in the great variety of corals sampled, exceeding any comparable collection from any locality known to the writer, the segregation of the decapod crustaceans according to coral host and individual coral head, and the accurate identification of the coral hosts by J.W. Wells, an internationally recognized authority.

Years of experience and expeditions to several of the world's coral-producing regions were required before the writer learned the importance of the simple procedures essential to success in this multidisciplinary endeavour: (1) the separation of the living coral from the dead, (2) the segregation of the live corals and their contained commensals according to host species, and (3) the retention of a fragment of each coral for later positive identification by a specialist. It is only when these procedures are adhered to consistently that reliable results can be expected bearing on host specificity, incipient speciation, competitive exclusion, recruitment, and predation. And while the procedures are not in themselves difficult, the patience to carry them out, frequently under less than ideal conditions, without lapses in technique, puts them beyond the accomplishment of any but the most seasoned collector.

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The coral community

The coral community is not one of the major environments characterized by J.D. Taylor in his comprehensive study of the coral reefs around Mahé, Seychelles (Taylor, 1968). Rather, it is a micro-environment found in several of the major ones. Were the corals themselves not listed, this could be deduced from Taylor's lists of the crustaceans commonly inhabiting them, of which the crab *Trapezia cymodoce* (Herbst) is found in sands and cobble ridges, reef edges and fronts, and deeper water outside reefs. This crab is an obligate symbiont of corals of the family Pocilloporidae, which must therefore occur in these major environments. Similarly, the crab *Tetralia glaberrima* (Herbst), listed for reef edges and fronts, and for deeper water outside reefs, is an obligate symbiont of corals of the family Acroporidae, which must therefore occur in these major environments, as indeed it does. Other obligatory symbionts listed by Taylor are the crabs *Trapezia guttata* Rüppell and *T. rufopunctata* Herbst, the shrimp *Alpheus lottini* (as *A. ventrosus* Milne Edwards), from reef edges and fronts, and the shrimp *Coralliocaris graminea* (Dana) from deeper water outside reefs as well. The first three are all associated with pocilloporid corals, the last with acroporid corals occurring in these major environments. The gall-crab *Hapalocarcinus marsupialis* and the burrowing crab *Cryptochirus coralliodytes,* listed from reef edges and fronts, are obligate symbionts of corals also, but are not included in the present report, as they were unrepresented among A.J. Bruce coral collections.

Each coral head, when placed on the cracking table (or, in the absence of such a table, on the nearest solid substrate, if only a slab of beach rock), is teeming with small invertebrates and fishes, which seek the coral branches for concealment, as a refuge from predators, or as a retreat for rearing their young. Some of these escape into the porous substrate; other retreat toward the base of the colony. Among the former are the ophiurans, or brittle-stars; among the latter are crabs of the genus *Cymo*, which occupy a shallow burrow in the coral's dead base. Between these extremes, and clinging to the branches, often with specially adapted dactyls, are the crabs of the genera *Trapezia* and *Tetralia* and the shrimps *Alpheus* and *Coralliocaris.*[1] These are invariably found in pairs unless one member has been dislodged by the tapping of the collector's hammer or manages to elude his probing forceps. The bright colors of these crustaceans, most frequently red, but often yellow, blue, green, or brown, serve no cryptic purpose, but flaunt themselves before predators, from which they are protected not only by the rasping branches, but by the myriad of nematocysts or stinging cells as well. Certain of the inquilines derive still other benefits from the corals, either sharing the particles of food rejected by their polyps, the commensals or mess-mates, or, in the case of *Trapezia* and *Tetralia*, by mascerating and eating the polyps themselves. These are the obligate symbionts, considered true parasites by

[1] For a complete listing of shrimps commensal with corals, see Bruce (1976).

Knudsen (1967), as they destroy the living tissues of the host.

The biologist who either lives in the tropics, or has seasonal access to a tropical marine laboratory, has the advantage of being able to observe the symbionts' manner of life. The museum taxonomist, with access only to preserved material, is restricted to speculating on the use of certain structures, patently adaptive, such as the claws of crabs and shrimps. Granted that errors in interpretation may occur, a large collection, well annotated, and containing specimens of different sexes and maturities, obtained at different times and places, from living coral as well as dead, and from corals of different families, genera, and species, provides many clues bearing on the host–symbiont relationship and the rigidity of the bond. It is such an analysis of the Seychelles coral community that the meticulously annotated collection of A.J. Bruce permits, which, when compared with the results from similar collections made in the Maldives and in the Marshall Islands by Garth (1967, 1974) and in Queensland by Patton (1966), will permit valid zoogeographical conclusions to be drawn.

Corals collected by A.J. Bruce in the Seychelles and Amirantes Islands

Corals were collected by A.J. Bruce in the Seychelles Islands at Anse Forban, Anse Etoile, North East Point, Anse aux Poules Blancs, Cerf Island, Port Glaud, Souris Island, Port Launay, Round Island, Victoria, and North West Bay, all on the island Mahé, and in the Amirantes Islands at Eagle Island. Of the 83 coral heads examined for decapod crustacean commensals, 46 were Pocilloporidae, 23 were Acroporidae, 7 were Poritidae, and one each were Agariciidae (*Pavona*), Thamnasteriidae (*Psammocora*), Milleporidae (*Millepora*), Helioporidae (*Heliopora*), and 3 were Oculiniidae (*Galaxea*). Corals were identified by John W. Wells as the following.

Pocilloporidae

Pocillopora damicornis (Linn.) (15 collections)
Pocillopora danae Verrill (1 collection)
Pocillopora elongata Dana (3 collections)
Pocillopora sp. indet. (1 collection)
Stylophora erythraea von Marenzeller (12 collections)
Stylophora mordax (Dana) (4 collections)
Stylophora cf. *S. mordax* (1 collection)
Stylophora pistillata (Esper) (8 collections)
Seriatopora hystrix Dana (1 collection)

Acroporidae

Acropora distincta (Brook) (1 collection)
Acropora cf. *A. diversa* (1 collection)
Acropora formosa (Dana) (3 collections)
Acropora haimei (Milne Edwards & Haime) (1 collection)
Acropora humilis (Dana) (2 collections)
Acropora cf. *A. humilis* (3 collections)
Acropora irregularis (Brook) (1 collection)
Acropora cf. *A. irregularis* (1 collection)
Acropora cf. *A. intermedia* (1 collection)
Acropora nana (Studer) (2 collections)
Acropora paniculata Verrill (1 collection)
Acropora squarrosa (Ehrenberg) (1 collection)
Acropora variabilis (Klunzinger) (5 collections)

Poritidae

Porites (*Synaraea*) *iwayamaensis* Eguchi (4 collections)
Porites n. sp. aff. *andrewsi* Vaughan (2 collections)
Porites n. sp. (= *P.* Maldives 2 of Bernard) (1 collection)

Agariciidae

Pavona danai (Milne Edwards & Haime) (1 collection)

Thamnasteriidae

Psammocora (Stephanaria) togianensis Umbgrove (1 collection)

Milleporidae

Millepora tenera Boschma (1 collection)

Helioporidae

Heliopora coerulea (Pallas) (1 collection)

Oculiniidae

Galaxea fascicularis (Linn.) (3 collections)

Methods of collecting

The methods of collecting crabs employed by A.J. Bruce were presumably the same as those used in collecting the shrimps that are his specialty, as both were extracted from the same coral heads. These methods were described in two letters dated 19 May and 2 June 1965, following the writer's experience in the Maldive Islands in March and April 1964 (Garth 1974), but preceding Dr. Bruce's visit to the Seychelles Islands during which the brachyurans here reported were collected. They are quoted here in full, as they represent an improvement on the writer's techniques, previously described. Dr. Bruce wrote as follows:

'I was very surprised by the paucity of *Periclimenes* [in your Maldivian collections], as these are usually abundant in corals. However, they are much more active than most of the species that you obtained, which tend to hang on to the coral until the last minute. When collecting shrimps I usually let them die in sea water and only then put them into preservative. I use formalin in the field and later transfer [them] to alcohol. Usually in the tropics they overheat and die quite soon, and as long as there are not too many in a tube, they do not break the legs off.

'I have been using large polythene bags to envelope the coral heads before breaking them off and then running the water through a net. This certainly enables the shrimp population to be more completely caught but has also provided me with quite a few crabs that I did not get otherwise. In particular I obtained a number [of] small crabs (*Thalamita*) which were adult although only 1/2" across the carapace. They were very active and dropped off the coral as soon as it was touched.'

It is assumed that these methods were the ones used by Dr. Bruce during his Seychelles Islands sojourn, perhaps with further refinements.

Coral commensals collected in Seychelles and Amirantes Islands, with frequency and manner of occurrence

In *Pocillopora damicornis* (13 heads):

Trapezia cymodoce (Herbst): 10 occurrences, 3 multiple, 7 as mated pairs (6 with females ovigerous)

Trapezia sp.[2] (fine-dotted): 8 occurrences, 1 multiple, 3 as mated pairs (2 with females ovigerous)

Trapezia guttata Rüppell: 4 occurrences, 1 multiple, 3 as mated pairs with females ovigerous

Trapezia ferruginea Latreille: 2 occurrences, 1 as mated pair with female ovigerous

Tetralia glaberrima (Herbst): 1 occurrence as a single young

Domecia hispida Eydoux & Souleyet: 1 occurrence as a single female

In *Stylophora erythraea* (8 heads):

Trapezia cymodoce (Herbst): 6 occurrences, 2 multiple, 5 as mated pairs (4 with females ovigerous)

Trapezia guttata Rüppell: 5 occurrences, 2 multiple, 3 as mated pairs with females ovigerous, 2 as single ovigerous females

Cymo andreossyi (Audouin): 3 occurrences, 1 as mated pair with ovigerous female, 1 as a single female

Trapezia sp. (fine dotted): 1 occurrence as a single young

Trapezia sp. aff. *wardi*: 1 occurrence as mated pair

In *Stylophora mordax* (5 heads) and *Stylophora* sp. cf. *S. mordax* (1 head);

Trapezia cymodoce (Herbst): 5 occurrences, 4 as mated pairs with females ovigerous

Trapezia ferruginea Latreille: 3 occurrences, 3 as mated pairs (2 with females ovigerous)

Trapezia sp. (fine-dotted): 1 occurrence as single young

Trapezia guttata Rüppell: 1 occurrence, multiple, with mated pair (female ovigerous)

Trapezia sp.: 1 occurrence, multiple, with mated pair (female ovigerous)

Cymo andreossyi (Audouin): 2 occurrences, 1 multiple, 1 as mated pair with female ovigerous

In *Stylophora pistillata* (4 heads):

Trapezia cymodoce (Herbst): 3 occurrences, 2 as mated pairs with female ovigerous, 1 single ovigerous female

Trapezia guttata Rüppell: 1 occurrence, multiple, with mated pairs (female ovigerous), and single ovigerous female

In *Pocillopora elongata* (2 heads):

Trapezia cymodoce (Herbst): 1 occurrence as mated pair (female ovigerous)

[2] Names used for the *Trapezia* species are in accordance with the key of Serène (1969), with the exception of the smaller, dotted species. As earlier shown by Ward (1939), *T. maculata* Dana comprised two species, now called *T. danai* Ward and *T. wardi* Serène, the first finely dotted, the second more coarsely dotted. Specimens from Sri Lanka and the Maldive Islands sent to Dr. Serène by the writer were returned as *T.* aff. *danai* and *T.* aff. *wardi*, indicating uncertainty concerning the conspecificity of Maldivian and western Pacific specimens of these species. The writer holds a similar view with respect to the Seychelles specimens, with the additional reservation that they may not be conspecific with the Maldivian either. The smaller, dotted species of *Trapezia* are in need of further review, which can only be done from fresh material, as the orange dots, which vary in size and number with the species, disappear after a few months in liquid preservative.

Trapezia ferruginea Latreille: 1 occurrence as single female
Trapezia ?digitalis Latreille: 1 occurrence, multiple, as single males
Domecia hispida Eydoux & Souleyet: 1 occurrence as mated pair and single female

In *Pocillopora danae* (1 head)
Trapezia cymodoce Herbst): 1 occurrence as mated pair with female ovigerous

In *Pocillopora sp. indet.* (1 head)
Trapezia cymodoce (Herbst): 1 occurrence as mated pair with female ovigerous

In *Seriatopora hystrix* (1 head):
Trapezia cymodoce (Herbst): 1 occurrence, multiple, as mated pair with female ovigerous, and as single ovigerous female
Trapezia ferruginea Latreille: 1 occurrence, as single male
Trapezia guttata Rüppell: 1 occurrence, multiple, as mated pair with female ovigerous, and as young

In *Acropora humilis* (4 heads) and *Acropora sp. cf. humilis* (1 head):
Tetralia glaberrima (Herbst): 5 occurrences, 4 as mated pairs with females ovigerous, 1 as single ovigerous female

In *Acropora variabilis* (4 heads):
Tetralia glaberrima (Herbst): 3 occurrences, one multiple, one as mated pair with female ovigerous, one as single ovigerous female
Tetralia heterodactyla Heller: 1 occurrence as single ovigerous female
Trapezia cymodoce (Herbst): 2 occurrences, 1 as single male, 1 as single young

In *Acropora nana* (2 heads):
Tetralia glaberrima (Herbst): 3 occurrences, 1 multiple, 2 as mated pairs with females ovigerous, 1 as single male
Cymo sp. indet.: 1 occurrence as single young

In *Acropora formosa* (2 heads):
Cymo andreossyi (Audouin): 2 occurrences, 1 as single female
Cymo melanodactylus Dana: 1 occurrence, multiple, as mated pair, single female, and young

In *Acropora* sp. (*variabilis* or *haimei*) (2 heads):
Tetralia glaberrima (Herbst): 1 occurrence as mated pair with female ovigerous
Cymo andreossyi (Audouin): 1 occurrence as single ovigerous female

In *Acropora irregularis* (1 head) and *A. sp. cf. irregularis* (1 head):
Tetralia glaberrima (Herbst): 2 occurrences as mated pairs with females ovigerous

In *Acropora sp. cf. intermedia* (1 head):
Cymo andreossyi (Audouin): 1 occurrence, as single male

In *Acropora haimei* (1 head):
Tetralia glaberrima (Herbst): 1 occurrence, multiple, as mated pair with

female ovigerous, single male, and single young.

Tetralia heterodactyla fusca Serène: 1 occurrence as single female

Cymo deplanatus Stimpson: 1 occurrence as single male

Cymo andreossyi (Audouin): 1 occurrence as mated pair

Domecia glabra Alcock: 1 occurrence as mated pair

In *Acropora disticha* (1 head):

Tetralia glaberrima (Herbst): 1 occurrence as mated pair with female ovigerous

In *Acrophora squarrosa* (1 head):

Trapezia cymodoce (Herbst): 1 occurrence, multiple, as mated pair with female ovigerous, and as mated pair

In *Acropora paniculata* (1 head):

Tetralia glaberrima (Herbst): 1 occurrence, multiple, as mated pair with female ovigerous, as single ovigerous female, and as single female

In *Galaxea fascicularis* (2 heads):

Cymo andreossyi (Audouin): 2 occurrences, 1 as single male, 1 as single female

Method of tabulating

The data from field collections are presented in a series of tables, each representing brachyuran crustaceans (crabs) collected from corals at a single locality in the Seychelles (Tables 1–11) or in the Amirante Islands (Table 12). Numbers of specimens of each brachyuran decapod species recovered from an individual coral head are arranged in a vertical column under the name of the coral host. Total numbers of brachyuran decapods collected from corals of each species at each locality sampled are carried to a Master Table, showing the occurrence of obligate commensals in branching corals of the Seychelles and Amirante Islands.

Note on nomenclature used

Some of the crab names here used are not those recently proposed by Guinot (1976), in which the older genus *Actaea* has been divided into a number of lesser genera. In this system *A. parvula* is referred to *Banareia (?), A. rufopunctata* to *Paractaea, A. tumulosa* to *Paractaea (?), A. rueppellii* to *Gaillardiellus, A. speciosa* to Aff. *Pseudoliomera,* and *A. tomentosa* to *Actaeodes*. Retention of the older terminology permits direct comparison with earlier work in Ceylon and the Maldives (Garth 1974a), and on the Great Barrier Reef (Patton 1966).

Host preferences of coral crabs

Crabs were found in 36 heads of coral of the family Pocilloporidae examined: in *Pocillopora damicornis* (13 heads), *Stylophora erythraea* (8 heads), *S. mordax* (5 heads), *S. pistillata* (4 heads), *Pocillopora elongata* (2 heads), and *P. danae, P. sp. indet.*, and *Seriatopora hystrix* (1 head each). Occurring consistently in all of these

Table 1 Ansc Forban, Mahé, 6 March 1966

	ACROPORIDAE (0)	POCILLOPORIDAE (3)		
		P. damicornis	*P. damicornis*	*P. damicornis*
Phymodius ungulatus		1		
Trapezia cymodoce		1	2	1
Trapezia ferruginea				1
Trapezia (fine-dotted)		1	2	1

Table 2 Anse Etoile, Mahé, 7, 23, 24, March; 19 April; 21 June 1966

	POCILLOPORIDAE							ACROPOR-IDAE			PORIT-IDAE	OCULINI-IDAE	
	S. erythraea	*S. erythraea*	*S. erythraea*	*S. erythraea*	*S. erythraea*	*S. erythraea*	*S. erythraea*	*A. humilis*	*A. nana*	*A.* cf. *irreg.*	*Porites* n. sp.	*G. fascicularis*	*G. fascicularis*
Actaea cf. *parvula*												1	
Chlorodiella nigra	1				6	10			1		1	1	1
Cymo andreossyi	2					2	1					1	1
Etisus frontalis	1												
Etisus laevimanus			1						1			1	
Leptodius exaratus													
Tetralia glaberrima								×	6	2			
Trapezia cymodoce	5	7		2		6	1						
Trapezia guttata		1	2	5	2	10							
Trapezia (fine-dotted)		1											
Trapezia aff. *wardi*						2							

was *Trapezia cymodoce*: in *Pocillopora damicornis* 10 times, in *Stylophora erythraea* 6 times, in *S. mordax* 5 times, in *S. pistillata* 3 times, and in *Pocillopora elongata, P. danae, P. sp. indet.*, and *Seriatopora hystrix* one time each. Occurring frequently in most of these was *Trapezia guttata*: in *Pocillopora damicornis* 4 times, in *Stylophora erythraea* 5 times, in *S. pistillata* 2 times, and in *S. mordax* and *Seriatopora hystrix* once each. (Its absence from *Pocillopora elongata* should be noted, perhaps in connection with the appearance there of *Trapezia digitalis*.) Also occurring frequently in several of these corals was a fine-dotted *Trapezia*: in *Pocillopora damicornis* 7 times, and in *Stylophora erythraea* and *S. mordax* once

Table 3 North East Point, Mahé, 8 March 1966

	POCILLOPORIDAE		ACROPORIDAE		
	P. danae	*P. damicornis*	*A. humilis*	*A. humilis*	*A. irregularis*
Phymodius nitidus	1				
Phymodius ? ungulatus		2			
Pilodius areolatus			1		
Tetralia glaberrima		1	4	2	7
Trapezia cymodoce	2				
Trapezia (fine-dotted)		2			

Table 4 Anse aux Poules Blancs, Mahé, 9 March 1966

		ACROPORIDAE	
	dead *Pocillopora*	*A. humilis*	*A. cf. inter.*
Actaea rüppellii	1		
Actaea tomentosa	2		
Carpilodes bellus	1		
Carpilodes tristis	1		
Cymo andreossyi			2
Phymodius monticulosus	2		
Tetralia glaberrima		2	

each. Occurring in several of these was *Trapezia ferruginea*: in *Pocillopora damicornis* 2 times, in *Stylophora mordax* 3 times, and in *Pocillopora elongata* and *Seriatopora hystrix* once each. Two rarely encountered *Trapezia* species were *T.* sp. aff. *wardi*: once in *Stylophora erythraea*; and *T.* sp. aff. *danai*, once in *S. mordax*. The occurrence of *Trapezia* in corals other than pocilloporid, particularly in Acroporidae, was rare. *T. cymodoce* was found twice in *Acropora variabilis* and once in *A. squarrosa*, where it was the only crab present. Such occurrence has been reported by other writers (Patton 1966). Thus it becomes evident that *Trapezia* has special affinities for pocilloporid corals, that the commonest species, *T. cymodoce*, occurs in corals of all three genera sampled, as does *T. guttata* less frequently, and that several species of *Trapezia* may occur in the same coral head. The small number of heads sampled of corals other than *Pocillopora damicornis* (and perhaps also *Stylophora erythraea*) makes it unwise

Table 5 Cerf Island, Mahé, 25 March, 18 May, 11 June 1966

	POCILLOPORIDAE						ACROPORIDAE	
	P. damicornis	*P. damicornis*	*S. hystrix*	*S. mordax*	*S. mordax*	*S. mordax*	*A. nana*	*A. nana*
Actaea rüppellii		1						
Chlorodiella nigra	1	3				1		
Cymo andreossyi						1		
Cymo sp.							1	
Etisus electra		2						
Etisus frontalis	1							
Etisus laevimanus		1						
Phymodius monticulosus	4	1						
Pilumnus vespertilio		1						
Tetralia glaberrima							3	2
Trapezia cymodoce	1	1	3	2	2			
Trapezia ferruginea			1	3	1			
Trapezia guttata			6					
Trapezia (fine-dotted)		1						
Menaethius monoceros						4		
Thalamita sp.		1						

Table 6 Port Glaud, Mahé, 7 April 1966

	POCILLOPORIDAE			ACROPORIDAE		MILLEPORIDAE
	P. damicornis	*P. damicornis*	*S. mordax*	*A.* cf. *humilis*	*A. variabilis*	*M. tenera*
Actaea tomentosa		2				
Lybia tessellata	1					
Phymodius nitidus						4
Phymodius ungulatus	1					
Tetralia glaberrima				2	1	
Trapezia cymodoce	2	4	2			
Trapezia ferruginea	2					
Trapezia guttata	1					
Trapezia (fine-dotted)	2					
Tylocarcinus styx				3		

Table 7 Souris Island, Mahé, 8 April 1966

	POCILLOPORIDAE	ACROPORIDAE (0)
	Pocillopora sp.	
Trapezia cymodoce	2	

Table 8 Port Launay, Mahé, 10 April, 6 May, 17 and 19 June, 1966

	POCILLOPORIDAE				OCULINIIDAE	HELIOPORIDAE
	P. damicornis	*P. damicornis*	*P. damicornis*	*P. damicornis*	*G. fascicularis*	*H. coerulea*
Carpilodes monticulosus			2		1	
Chlorodiella cytherea	1					
Chlorodiella laevissima					1	
Domecia hispida	1					
Lophozozymus pulchellus	1					
Phymodius monticulosus				2		
Pilodius areolatus	1					
Trapezia cymodoce	4	4	14	7		
Trapezia guttata	2		4			
Trapezia (fine-dotted)	2			2		
Thalamita sp.						1

to speculate concerning host specificity of *Trapezia* for corals at the generic or specific level.

Crabs occurred in 21 heads of corals of the family Acroporidae examined: in *Acropora humilis* and *A. sp. cf. humilis* (4 and 1 heads), *A. variabilis* (4 heads), *A. nana, A. formosa,* and *A. sp.* (*variabilis* or *haimei*) (2 heads each), *A. irregularis, A. sp. cf. irregularis, A. haimei, A. disticha, A. squarrosa, A. paniculata* (one head each). Consistently present in all corals except *A. formosa, A. sp. cf. intermedia,* and *A. disticha* (and the previously mentioned *A. squarrosa*, in which *Trapezia cymodoce* was found), was *Tetralia glaberrima*: in *A. humilis* and *A. sp. cf. humilis* 5 times, in *A. variabilis* 3 times, in *A. nana* 3 times, and in *A. sp.* (*variabilis* or *haimei*), *A. sp. cf. irregularis, A. haimei, A. disticha*, and *A. paniculata* one time each. Occurring rarely were *Tetralia heterodactyla*, once in *A. variabilis*, and *T. heterodactyla fusca,* once in *A. haimei.* The occurrence of *Tetralia* in corals other than acroporid, particularly among Pocilloporidae, was

Table 9 Round Island, Mahé, 13 April 1966

	POCILLOPORIDAE	ACROPORIDAE					
	S. mordax	*A. disticha*	*A. formosa*	*A. haimei*	*A. variabilis*	*A. variabilis* or *A. haimei*	*A. variabilis* or *A. haimei*
Actaea nr. *tumulosa*	1						
Chlorodiella nigra							1
Cymo andreossyi				2		1	
Cymo deplanatus				1			
Cymo melanodactylus			1				
Domecia glabra				2			
Phymodius sp.		1			1		
Pilodius sp.	1						
Tetralia glaberrima		2		7	12		2
Tetralia heterodactyla					1		
Tetralia h. fusca				1			
Trapezia cymodoce	2						
Trapezia digitalis	2						
Trapezia ferruginea	4						
Trapezia (fine-dotted)	1						
Trapezia sp.	4						
Tylocarcinus styx						1	

Table 10 Victoria, Mahé, 17 May, 3 June, 1966

	POCILLOPORIDAE								ACROPORIDAE					PORITIDAE		
	P. damicornis	*P. damicornis*	*S. pistillata*	*S. pistillata*	*S. pistillata*	*S. pistillata*	*S. erythraea*	*S.* cf. *mordax*	*A. formosa*	*A. paniculata*	*A. squarrosa*	*A. variabilis*	*A. variabilis*	*P.* n. sp.	*P.* n. sp.	*P. iwayamaensis*
Actaea rufopunctata			1													
Chlorodiella nigra	1	5			1			3		1			1	2	10	1
Cymo andreossyi								5	3							
Tetralia glaberrima										5						
Trapezia cymodoce			1		3	2		2			4	2	2			
Trapezia guttata		2	3	1			3	4								
Trapezia (fine-dotted)	1															

Table II North West Bay, Mahé, 23 May 1966

	POCILLOPORIDAE	ACROPORIDAE (0)
	P. elongata	*P. elongata*
Carpilodes rugipes		2
Cymo cf. *quadrilobatus*		1
Domecia hispida		2
Phymodius ?granulosus		2
Pliodius wood-masoni	1	
Pilumnus sp.		1
Trapezia cymodoce		2
Trapezia ?digitalis		2
Trapezia ferruginea		1

rare. *T. glaberrima* was found once in *Pocillopora damicornis,* together with the fine-dotted *Trapezia* sp. The single specimen was a juvenile. It is therefore apparent that *Tetralia* has special affinity for acroporid corals, that the commoner species, *T. glaberrima,* occurs in most *Acropora* species, and that the uncommon *T. heterodactyla* and *T. h. fusca* may occur with it in the same coral head. The small number of heads of each species of *Acropora* sampled makes it inadvisable to speculate concerning host specificity of *Tetralia* for corals at the specific level. Such specificity, if it exists, might apply to the named varieties of *T. glaberrima* (Patton 1966), of which several were distinguished among Seychelles specimens.

Two other genera of xanthid crabs known to be obligatory symbionts of corals were present in the collection studied: *Cymo* and *Domecia*. Of them only *Domecia* appears to exhibit consistently in the Seychelles the host specificity reported for it elsewhere (Patton 1966, Garth 1974). Thus *D. hispida* was found in the pocilloporid corals *Pocillopora damicornis* and *P. elongata* (one head each), while *D. glabra* was found in the acroporid coral *Acropora haimei* (one head). Of the *Cymo* species, the separation of the 'light-fingered' *C. andreossyi* from the 'dark-fingered' *C. melanodactylus* proved difficult on the basis of claw color alone, many specimens having either dark fingers with light tips or white fingers with dark bases. When, however, the specimens were segregated according to the color of the scattered granules of the carapace, as suggested by Patton (*op. cit.*), the only specimen with orange granules proved also to be the only specimen with jet-black claws. Here recognized as *C. melanodactylus*, it was found in the acroporid coral, *Acropora formosa*. The remaining specimens with white granules included those with both light and dark fingers, the tips of which were always white. Here recognized as *C. andreossyi,* they came from both pocilloporid and acroporid corals: *Stylophora erythraea* 3 times, *S. mordax* twice; *Acropora formosa* twice, and *A. haimei* and *A. sp. cf. intermedia* once each. *C. andreossyi* was

also found twice in the oculiniid coral *Galaxea fascicularis*. *Cymo* sp. cf. *quadrilobatus* was found once in *Pocillopora elongata* and *C. deplanatus* once in *Acropora haimei*, while *Cymo* sp., a young specimen, was found once in *A. nana*. Thus, while it may be said that of the four *Cymo* species encountered in Seychelles corals, *C. andreossyi* and *C.* sp. cf. *quadrilobatus* show preference for pocilloporid corals, *C. melanodactylus* and *C. deplanatus* for acroporid corals, the preference of *C. andreossyi*, if correctly identified in all cases, it not as rigid as has been found previously, with considerable latitude in choice of host families apparent.

Incidence of pairing

In considering which crabs are obligate commensals and which are facultative or adventitious in corals, the presence of mated pairs in which the female is ovigerous is of paramount importance. Thus *Trapezia cymodoce*, with affinities for pocilloporid corals, was present as a mated pair (or pairs) in 22 of the 30 coral heads in which the crab was present. If to this number the corals in which ovigerous females alone were found be added, the number increases to 25 of the 30. Multiple occurrences of mated pairs with ovigerous females were restricted to the larger corals: in *Pocillopora damicornis* 2, 3, and 4 pairs; in *Stylophora* no more than 2 pairs per head. Similar strong affinities for pocilloporid corals are shown by *Trapezia guttata*, present as a mated pair (or pairs) in 9 of the 14 coral heads in which the crab occurred. If to this number the corals containing only ovigerous females be added, the number increases to 12 of the 14. Multiple occurrences were also noted: in *Stylophora* 2 mated pairs (twice) and 4 mated pairs (once); in *Seriatopora* 2 mated pairs (once). The fine-dotted *Trapezia* was less frequently found as a mated pair (or pairs): in 4 of 11 coral heads in which the crab was found, each case in *Pocillopora damicornis*. Of these one was a multiple occurrence, with 2 pairs present; of more frequent occurrence were young or single males and non-ovigerous females, presumbly adventitious. Two other *Trapezia* spp., *T. aff. danai* and *T. sp.*, occurred as mated pairs in one instance each, both in *Stylophora*. *Trapezia digitalis* was present as a mated pair with female ovigerous in *Stylophora mordax*, and as unattached males (2) in *Pocillopora elongata*. Thus a good case can be made for *Trapezia* species as obligate commensals based on the presence of numerous mated pairs.

The case for *Tetralia* species as obligate commensals of acroporid corals is equally compelling. *T. glaberrima* was present as a mated pair (or pairs) in 13 of the 16 coral heads in which the crab occurred, and as a single ovigerous female in one other. Multiple occurrences were found in *Acropora variabilis*: 3 mated pairs (once), and in *A. haimei* and *A. nana*: 2 mated pairs (once each). As many as 6 young were found in a single head of *A. variabilis*, 5 young in a single head of *A. irregularis*. *T. heterodactyla* was found once as an ovigerous female in *A. variabilis* and once as a non-ovigerous female in *A. haimei*.

Degree of affinity for the coral host

The finding of an ovigerous female (or females) in a head of living coral does not of itself make that crab an obligate commensal. It must also be demonstrated that the species does not also occur in dead coral, or in rocky or rubbly substrate providing the same opportunity for concealment to the brooding female. Fortunately, a collection of crabs from dead *Pocillopora* was made by Dr. A.J. Bruce at Anse aux Poules Blancs, Mahé (Sta. No. 4, 9 March 1966). This allows us to eliminate three *Actaea* species: *A. ruppellii, A. tomentosa*, and *A.* sp. cf. *tumulosa*, and three *Carpilodes* species, *C. bellus, C. monticulosus*, and *C. tristis*, as obligate symbionts of living corals, as they are also found in dead corals. Beyond this, we can turn to the lists of Seychelles invertebrates according to environments prepared by Dr. J.D. Taylor (1968), from which we can eliminate *Etisus electra,* present in ex-mangrove fringes, sands and cobble ridges, and algal ridge; *Leptodius exaratus*, in grass beds, sands and cobble ridges, and algal ridge; *Actaea tomentosa,* in sands and cobble ridges, algal ridge, and reef edges; *Phymodius monticulosus*, in grass beds and algal ridge; *Carpilodes monticulosus*, in sands and cobble ridges; *Chlorodiella nigra* and *Pilumnus vespertilio*, in grass beds; *Pilodius areolatus,* in algal ridge; *Actaea parvula* and *Chlorodiella nigra,* from deeper water outside reef. Beyond this point, in lieu of habitat-documented collections from the Seychelles, the writer would refer to his own collecting experiences in Sri Lanka and the Maldive Islands; however, it will be noted that the above exclusions include at least one member of each genus collected in corals in the Seychelles by Dr. A.J. Bruce with the exception of *Lophozozymus* and *Lybia*. The former inhabits rocky or rubbly substrates; the latter is a symbiont, not of stony corals, but of actinians that it carries about, one in each chela, and from whose rejected food particles it obtains a portion of its diet. In general, one species can be taken as representative of its genus insofar as affinities for corals are concerned, an important exception being *Actaea speciosa*, found by A.J. Bruce in the Amirante Islands in *Pocillopora damicornis* (Table 12), which alone of its congeners shows a structural modification of one of its dactyls for a corallicolous existence.

We are left, then, with the xanthid crab genera *Cymo, Domecia, Tetralia,* and *Trapezia* as obligate commensals with living corals from among the collection studied. While *Maldivia* and *Quadrella* are xanthid genera of similar habit, the latter associated with gorgonian corals, these were not included in the Bruce collection. Only the aforementioned genera are used in discussing relationships between the coral-inhabiting fauna of the Seychelles and those of other islands or island groups.

Seychelles and Maldives collections compared

Although the present study includes only the crabs, whereas the writer's earlier studies of decapods commensal with reef-building corals in Sri Lanka and the Maldives (Garth, 1974) included both crabs and shrimps, certain comparisons will be useful. First, a wider selection of corals was sampled in the Seychelles than in the Maldives. These included not only members of the families Pocilloporidae and Acroporidae, but also members of the families Oculiniidae, Poritidae, Agariciidae, Thamnasteriidae, Milleporidae, and Helioporidae. However, with the exception of the Oculiniidae, these added families yielded no crabs not also found in other corals, dead as well as living, and in rocky and rubbly substrates. The Oculiniidae, represented by *Galaxea fascicularis*, yielded a species of *Cymo* known to be an obligate commensal of corals, plus two species of Actaeinae with high affinity for corals. Second, the method of sampling used in the Seychelles, in which each coral head was first enclosed in a plastic bag before the coral was loosened from the substrate, insured recovery of the particularly sensitive forms that leave the coral at first sign of disturbance. These include not only shrimps of the genus *Periclimenes*, but also crabs of the genus *Thalamita* and others. Third, corals of the family Pocilloporidae are better represented in the Seychelles collection, including, in addition to *Pocillopora*, the genera *Stylophora* and *Seriatopora*. This may not be as significant as appears, however, because host specificity of crabs for corals appears to be at the familial, rather than generic level. At five of the ten localities at which corals were sampled in Sri Lanka and the Maldives (five of nine if Sri Lanka be excepted) no pocilloporids were included, although effort was made to achieve a balance between the two families when possible. On the other hand, pocilloporid corals were obtained from every locality in the Seychelles, while at nearly half (Anse Forban, Cerf Island, Souris Island, Port Launay, North West Bay), acroporid corals were not sampled.

Crabs found to be obligate commensals of pocilloporid corals were *Cymo quadrilobatus, Domecia hispida, Trapezia cymodoce, T. ferruginea, T.* aff. *wardi, T.* aff. *maculata, T.* aff. *danai*, and *T. digitalis*. Crabs found to be obligate

Table 12 Eagle Island, Amirantes, 30 March 1966

	POCILLOPORIDAE	ACROPORIDAE (0)
	P. damicornis	
Actaea speciosa (Dana)	3	
Trapezia cymodoce Herbst	6	
Trapezia (fine-dotted)	1	

commensals of acroporid corals were *Cymo deplanatus, C. melanodactylus, Domecia glabra, Tetralia glaberrima, T. heterodactyla,* and *Trapezia cymodoce* (2 occurrences, perhaps adventitious). Of the *Trapezia* species, *T.* aff. *maculata* was absent from the Seychelles, and it is by no means certain that the *T.* aff. *danai* is the same in both localities. Species found in the Seychelles but absent from the Maldives were *Cymo andreossyi* and *Trapezia guttata.*

Seychelles and Great Barrier Reef collections compared

Earlier studies by Patton (1966) on decapods commensal with branching corals of the Great Barrier Reef provide material for a comparison of Seychelles commensals with those from the western South Pacific Ocean. Both crabs and shrimps were included in Patton's study. Corals were limited to the families Pocilloporidae and Acroporidae, but of the former the genera *Stylophora* and *Seriatopora* were included in addition to the genus *Pocillopora*, whereas the species of the genus *Acropora* were not distinguished from one another. Method of collecting was to lift the coral head on a screen to a portable table, where it was cracked, thus providing a solid substrate through which the decapods could not escape. Crabs found to be obligate commensals of the Pocilloporidae were *Cymo andreossyi, Domecia hispida, Trapezia cymodoce, T. ferruginea, T. areolata, T. guttata, T. digitalis,* and *T. rufopunctata.* Crabs found to be obligate commensals of the Acroporidae were *Cymo melanodactylus, C. deplanatus, Domecia glabra, Tetralia glaberrima,* and *T. heterodactyla,* including *T. h. fusca.* Patton recognized a number of colour forms of *T. glaberrima*, several of which occur also among Seychelles collections. The same preferences for coral hosts were noted among Seychelles commensals, except that for the *Cymo* species the host specificity appeared less rigid. This does not nullify the observations of Patton, but indicates that additional work is needed on *Cymo* in the Seychelles. Of the *Trapezia* species, *T. areolata* was absent from the Seychelles, as was also *T. rufopunctata.* Species present in the Seychelles but absent from Patton's Great Barrier Reef collection were *Trapezia* aff. *danai* and *Trapezia* aff. *wardi*, and also *Trapezia* sp.

Seychelles and Eastern Pacific collections compared

As has been pointed out previously (Garth 1974), corallicolous crabs and shrimps are with few exceptions the only decapod crustacean species common to both the western and eastern Pacific oceans. That the same statement holds true for the western Indian and eastern Pacific oceans is even more remarkable. As more is learned of the free-living crabs of presumed pan-tropical distribution, these have been partitioned between the eastern and western hemispheres. Formerly con-

Table 13 Brachyura collected from corals at all stations – Mahé, Seychelles and Amirantes, March-June 1966

	POCILLOPORIDAE									ACROPORIDAE														OC*
	Dead *Pocillo.* (1)	*P. damicornis* (13)	*P. danae* (1)	*P. elongata* (2)	*Se. hystrix* (1)	*St. erythraea* (8)	*St. mordax* (5)	*St. cf. mordax* (1)	*St. pistillata* (4)	*A. disticha* (1)	*A. formosa* (2)	*A. haimei* (1)	*A. humilis* (4)	*A. cf. humilis* (1)	*A. irregularis* (1)	*A. cf. irregularis* (1)	*A. cf. intermedia* (1)	*A. nana* (3)	*A. paniculata* (1)	*A. squarrosa* (1)	*A. variabilis* (4)	*A. var./haimei* (2)	*G. fascicularis* (2)
Trapezia cymodoce		54	2	2	3	21	8	2	6											4	4		
Trapezia digitalis				2			2																
Trapezia ferruginea		3		1	1		8																
Trapezia guttata		9			6	23	3	4	6														
Trapezia (fine-dotted)		12				1	1																
Trapezia aff. *wardi*						2																	
Trapezia sp.						4																	
Tetralia glaberrima		1								2		7	10	2	7	2		11	5		13	2	
Tetralia heterodactyla																					1		
Tetralia h. fusca												1											
Cymo andreossyi						5	6	5			3	2					2						2
Cymo deplanatus												1											
Cymo melanodactylus											1												
Cymo cf. *quadrilobatus*				1																			
Domecia glabra												2											
Domecia hispida				2																			

* OCULINIIDAE

sidered circumtropical, the well known shore crab, *Grapsus grapsus* (Linnaeus), is now divided into the eastern Pacific-Atlantic *G. grapsus* and the Indo-West Pacific *G. tenuicrustatus* (Herbst). As more is learned of the coral-inhabiting species, these have been shown to be one-and-the-same species, east and west. Seychelles coral crabs also found in the eastern tropical Pacific include *Domecia hispida, Trapezia digitalis, T. ferruginea,* and possibly *T. danai,* in addition to the coral-gall crab, *Hapalocarcinus marsupialis.* Seychelles coral shrimps include *Alpheus lottini,* formerly *A. ventrosus.* These are all obligate symbionts of corals of the family Pocilloporidae, of which *Pocillopora damicornis* is now recognized as occurring on both sides of the so-called Central Pacific Barrier. One theory holds that the reason the crabs survive after their lengthy trip (encompassing many generations) as larval stages is that they find in the new locality the microhabitat to which they were adapted in the old (Patton 1966:293). The absence of a *Tetralia* species, or of *Domecia glabra,* which likewise prefers *Acropora* coral, is due to the absence from the eastern Pacific of the coral family Acroporidae, rather than the inability of their larval stages to cross the Pacific Barrier. The coral community may be seen, therefore, to have a remarkably similar aggregation of decapod crustacean species, of which those of the *Pocillopora* colony extend from the shores of east Africa and its satellite islands, the Seychelles, to the shores of western America and its satellite islands, of which the Galapagos are perhaps the best known. And wherever found, it provides a remarkably stable environment for the same relatively few obligate residents, while providing shelter for the many chance residents which vary according to species from place to place.

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Addendum

Since the present chapter was completed in early 1979, the names proposed for xanthid genera by Guinot (1969, 1976) have come into general use and were, in fact, adopted by the present author for the Philippine Xanthidae (Garth & Kim 1983). Rather than making extensive changes in proof, it has been thought better to retain the older terminology, which allows for direct comparison with earlier work on Ceylon and the Maldives (Garth 1974a), and on the Great Barrier Reef (Patton 1966), and to give a table equating the older names with the newer:

Older Name	Current Name
Actaea parvula	*Banareia (?) parvula*
Actaea rufopunctata	*Paractaea rufopunctata*
Actaea rueppellii	*Gaillardiellus rueppellii*
Actaea speciosa	aff. *Pseudoliomera speciosa*
Actaea tomentosa	*Actaeodes tomentosus*
Actaea tumulosa	*Paractaea (?) tumulosa*
Carpilodes bellus	*Liomera bella*
Carpilodes monticulosus	*Liomera monticulosa*
Carpilodes rugatus	*Liomera rugata*
Carpilodes rugipes	*Liomera rugipes*
Carpilodes tristis	*Liomera tristis*

The genus *Trapezia* is currently being revised by B. Galil, who writes (letter of 21 July 1982) that specimens of the author's collecting in the Maldives identified by the late R. Serène as '*T.* aff. *danai*' and '*T.* aff. *warci*' are in her opinion the young of *T. tigrina* Eydoux and Souleyet. It follows that Seychelles material of these two species identified by the author using Serene's (1969) key should probably be referred to *T. tigrina* also.

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