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ON THE OCCURRENCE IN THE EASTERN TROPICAL PACIFIC OF INDO-WEST PACIFIC DECAPOD CRUSTACEANS COMMENSAL WITH REEF-BUILDING CORALS

John S. Garth

Allan Hancock Foundation¹ University of Southern California, Los Angeles, California 90007

SUMMARY

Corallicolous crabs have been known from the eastern tropical Pacific since the middle of the nineteenth Century. Described originally as new species, they have increasingly been found identical with Indo-west Pacific species; in fact, with few exceptions, corallicolous crabs and shrimps are the only decapod crustacean species common to both western and eastern Pacific oceans. Host specificity is believed to account best for the presence or absence of Indo-west Pacific reasons are excluded from these regions.

Methods are considered by which fragile larval stages may have transgressed the formidable mid-Pacific oceanic barrier and established themselves on opposite shores. It is concluded that coral commensals have succeeded where free-living species have failed because, once found, the coral community provides the habitat to which they are uniquely pre-adapted, whereas the free-living species must modify themselves to meet a variety of conditions that may differ markedly from the cold.

I. HISTORICAL ACCOUNT

A. SPECIES PRESENT

1. The first of the coral-inhabiting species of Xanthidae from the eastern Pacific was reported by Gerstaecker (1857). Specimens were collected in Veragua, Panama, by von Warscewicz, and were deposited in the Berlin Museum. Gerstaecker considered them to represent a new species, which he described as *Trupezia corallina*, now recognized as a synonym of the Indo-west Pacific *T. digitalis* Latreille.

2. The second of the coral-inhabiting species of Xanthidae from the eastern Pacific was reported by Stimpson (1860). Specimens reportedly collected at Socorro Island, Mexico, one of the Revilla Gigedo Islands, were forwarded to Stimpson by J. Xantus, keeper of the light at Cape San Lucas, who, as far as is know, did not visit these islands himself. These were reported by Stimpson as *Trapezia maculata* Dana (not MacLeay), a species now known as *T. danai* Ward, and were probably collected in Hawaii, since no spotted *Trapezia* species has been reported from the Revilla Gigedo Islands (or elsewhere in the eastern Pacific) since.

3. The third of the coral-inhabiting xanthids from the eastern Pacific was reported by S. I. Smith (1869). Specimens were collected at Pearl Islands, Bay of Panama, by F. H. Bradley, and were referred by Smith with a question mark to

¹Allan Hancock Foundation Contribution No. 350.

Trapezia cymodoce Guérin, following Dana (1852b). With them were collected in somewhat lesser abundance, but also in *Pocillopora capitata* Verrill, specimens of the species described earlier by Gerstaecker, which Smith also assumed to be new and described as *Trapezia formosa*.

4. The fourth species and second genus of coralinhabiting Xanthidae from the eastern Pacific, *Quadrella nitida*, was described by S. I. Smith (1869). Types were collected at Pearl Islands, Bay of Panama, by F. H. Bradley, and although reported from among pearl oysters, the species is known to occur on the gorgonian coral, *Muricea miser* Verrill (Crane, 1937).

5. The fifth species and third genus of coralinhabiting Xanthidae from the eastern Pacific, *Domecia hispida* Eydoux and Souleyet, was reported by Verrill (1908) from between branches of *Pocillopora* on the Gulf of California and Panama. A companion species, *Domecia acanthophora* Desbonne and Schramm (1867), was described from the island of Guadaloupe in the Caribbean, where it occurs on *Acropora* (Rathbun, 1921) and in beds of *Porites* (Rathbun, 1930; Patton, 1967).

6. The sixth species and fourth genus of coralinhabiting Xanthidae from the eastern Pacific, *Maldivia galapagensis*, was described by Garth (1939) from *Pavona* coral collected in the Galapagos Islands by the Hancock Expedition of 1938. Assumed at the time to be a Galapagos endemic species, it was discovered later among mainland

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collections obtained at Port Parker, Costa Rica (unpublished record), by the Hancock Expedition of 1934, of which Garth was also a member.

7. Although the discovery in the eastern Pacific of the coral commensal crabs Trapezia and Domecia took place in the mid-19th Century, the discovery of the coral gall-forming and burrowing Hapalocarcinidae is much more recent, dating from the mid-20th century. Thus, while Hapalocarcinus marsupialis was described by Stimpson from Hilo, Hawaii, in 1859, and was widely known in the Indo-west Pacific, including Murray Island on the Great Barrier Reef (Potts, 1915), it was first found in the New World at Port Utria, Colombia, in 1934 by Waldo L. Schmitt of the Smithsonian Institution of one of the Hancock Expeditions of which Garth was also a member (Schmitt, 1936). It has since been taken at Clipperton Island in 1958 by E. S. Reese, T. Chess, and A. Hambly (Garth, 1965), invariably in *Pocillopora* coral.

8. Similarly, while *Cryptochirus crescentus* was described by Edmondson from Johnston Island in the mid-Pacific in 1925, it was not until 1958 that C. Limbaugh and E. C. Allison discovered the species at Clipperton Island (Garth, 1965), and not until 1968 that G. F. Crozier, while diving off El Tule Ranch, 10 miles E. of Cape San Lucas, Baja California, recovered the species from the North American mainland (Garth and Hopkins, 1968), all recoveries being from *Pavona* coral. A coralburrowing species, *Cryptochirus corallicola* (Verrill), is also known from the Caribbean, where it occurs in the coral *Meandra*.

B. GENERA AND SPECIES ABSENT

1. Genera Absent.

Of equal significant from a distributional standpoint to the genera and species of Indo-west Pacific coral commensals found in the eastern Pacific are the genera and species not found there. The most important omission to one familiar with the fully developed Indo-West Pacific coral fauna is the genus *Tetralia*, which occupies in acroporid corals a niche analogous to that of *Trapezia* in pocilloporid corals (Garth, 1964, 1971; Patton, 1966). The absence of *Tetralia* from the eastern Pacific coincides with the absence of corals of the family Acroporidae. These occur in the Caribbean, however, where *Tetralia* is also absent (Garth, 1968).

Next to *Tetralia*, in point of significance, is the absence from the eastern Pacific of *Domecia glabra* Alcock, one of two Indo-west Pacific species of *Domecia*. This again coincides with the absence of acroporid corals, for *D. hispida*, the second Indo-west Pacific species, occurs in the eastern Pacific, together with its pocilloporid coral hosts.

A third species, *D. acanthophora* Desbonne and Schramm, occurs in the Caribbean, where *Acropora*, but not *Pocillopora*, is found.

C. HOST SPECIFICITY

1. Degree of Specificity

It will be seen from the foregoing that the coral commensals are host-specific, and also that the specificity of the genus *Tetralia* is for the family *Acroporidae*, that of *Trapezia* for the Pocilloporidae, while the species of *Domecia* are limited to one or other of the two coral families (Garth, 1964, p. 142). The host specificity of *Maldivia* must be inferred, as specimens of *M. galapagensis* were recovered from water in which *Pavona* had been rinsed (Garth, 1939), rather than *in situ*. According to A. J. Bruce (personal communication) the host of *M. triunguiculatus* of the Indo-west Pacific is *Galaxea*.

2. Age of Relationship

A further conclusion is that the host specificity of *Tetralia* for *Acropora*, and of *Trapezia* for *Pocillopora* or other pocilloporid corals, is an older relationship than that of *Domecia glabra* for *Acropora* and *D. hispida* for *Pocillopora*, since entire genera of crabs are involved, rather than species of one genus (Garth, 1964, p. 144).

3. Common Occurrence

A further important consideration is that the species of *Trapezia (T. ferruginea, T. digitalis,* and questionably, *T. danai)* that occur in the eastern Pacific are those that also occur in the Indo-west Pacific. The same is true of *Domecia hispida,* but not, apparently, of *Quadrella nitida* and *Maldivia galapagensis* (although the relationship of the former with the Indo-west Pacific *Q. coronata* and of the latter with the Indo-west Pacific *M. triunguiculatus* is a close one). A similar relationship exists among shrimp of the families Alpheidae and Palaemonidae, subfamily Pontoniinae, where *Alpheus lottini* and *Fennera chacei*, commensals of Pocilloporidae, occur in both Indo-west Pacific and eastern Pacific oceans (Patton, 1966; Bruce, 1965).

D. METHOD OF TRANSPORT

With the exception of a few facultative species also associated with corals, of which *Liomera cinctimana* (White) is one, the coral commensals are the only decapod species known to have transgressed the Central Pacific Oceanic Barrier (Ekman, 1953). How they may have done this is the subject of the second half of this paper. The factors involved are (1) tremendous distances, measured in thousands of miles, (2) profound depths, measured in thousands of meters, (3) ocean currents, both surface and sub-surface, travelling at speeds of from one to several knots, and capable of transporting (4) larval stages of decapod crustaceans, whose life-span is but a few weeks, to and from (5) islands and atolls, serving as present-day stepping stones for current-borne larval stages, (6) submerged seamounts or guyots that may have served as stepping-stones in the past, the shallower of them exposed by (7) inter-glacial fluctuations in sea-level, particularly during the Pleistocene, with (8) concomitant temperature and salinity changes that may have locally exterminated corals and their crustacean inhabitants, (9) trans-Isthmian connections during Miocene-Pliocene that may have altered the direction of ocean currents, alternating with inter-continental bridges that may have excluded corals or commensals from the Caribbean or Bay of Panama, and (10) ocean-floor spreading that has increased the separation between the eastern and western Pacific faunas over extended periods of time. Each of these factors will be examined for its bearing on the present distribution of the coral-commensal crabs.

1. Distance

Fortunately, it is not necessary to consider the 6,000-mile distance between the coast of Queensland and its Great Barrier Reef and the west coast of America, but only the 2,000-mile distance between the most easterly of the Polynesian islands and the island outliers of the Americas. The Polynesian islands are Hawaii, the Line Islands, the Marquesas, and Tuamotu. These trend in a northwesterly to south-easterly direction that parallels the coast of North and South America and its island outposts of Clarion, Clipperton, and the Galapagos. Only in the far south is this oceanic barrier bridged by a series of islands: Pitcairn, Ducie, Easter, Sala-y-Gomez, San Felix and San Ambrosio (Garth, 1973), all of which lie below the Tropic of Capricorn.

2. Depth

Oceanic islands are, by definition, separated from each other and from adjacent continents by abyssal depths of 1000 fathoms or more (Wallace, 1880; Garth, 1967). Classic examples are Hawaii and the Galapagos, but the Revilla Gigedo Islands are strictly comparable.

3. Ocean currents

The predominant currents of the tropical eastern

Pacific are westerly directed, the North and South Equatorial currents being part of the respective North and South Pacific gyres, the northern gyre clockwise, and the southern gyre counter-clockwise in circulation. Between them, however, and displaced slightly north (6-10 deg.) of the Equator, is the easterly-directed Equatorial Counter Current. Beneath the South Equatorial Current, at a depth of 100 meters, lies the recently discovered Cromwell Current (Cromwell *et. al.*, 1954) which has been traced 3,500 nautical miles from the Marquesas to the Galapagos Islands. The speed of these currents, which fluctuate widely, is from one to three knots, or from 24 to 72 nautical miles per day.

4. Larval stages

Because most marine laboratories are located in temperate regions, few tropical crab species have been reared through their life stages of egg, zoea, megalopa, and adult. While there is only one of each of the other stages, there may be from three to five or more zoeal stages. Four weeks is commonly required from egg to adult, with development prolonged at lower temperatures or in the case of those with a greater number of zoeal stages. Starvation also retards metamorphosis (Passano, 1960), and some invertebrates can postpone metamorphosis until conditions are favorable for settling (Wilson, 1952). A crab larva travelling in a 3-knot current for 28 days (4 weeks), or a crab larva travelling in a 2-knot current for 42 days (6 weeks) would both cover a distance of 2,016 nautical miles, which would bridge the largest gap between islands, or island and mainland.

5. Island stepping-stones

Islands or archipelagoes serving as steppingstones for current-borne larval stages in the eastern Pacific are the Revilla Gigedo Islands (Clarion, Socorro, San Benedicto) and Clipperton Island off Mexico; Cocos and Malpelo Islands off Panama; the Galapagos Islands off Ecuador; and Easter Island off Chile. These vary in distance from but a few hundred miles (Cocos, Socorro) to 2,000 miles (Easter Island). Definitive reports are available on the Brachyura of the Galapagos (Garth, 1946), Clipperton (Garth, 1965), and Easter Island (Garth, 1973). It is significant that each of the coral commensal crabs recorded from the American mainland is also present at one or more of these island outliers, which may have served as points of entry.

In addition to the distant outliers of the Americas, there are islands of continental origin so close to the mainland that it would seem pointless to distinguish them. Yet it is at these very islands that the so-called "mainland" records of both corals and coral-inhabiting decapods occur, probably because their short remove from the mainland suffices to clear them of the detritus arising from the numerous rivers of middle America, which carry a tremendous runoff during the rainy season. Such inshore insular localities as Secas Islands, Panama; Gorgona Island, Colombia; and La Plata Island, Ecuador; are therefore given in the systematic account that follows, together with the Cape San Lucas region of Baja California, which constitutes an island for warm-water species.

6. Submerged seamounts

Echo-sounding devices have made it possible to probe the depths of the ocean with a detail and accuracy not possible with manual sounding. One of its dividends has been the discovery of hundreds of submerged mountain peaks (Hess, 1946). These were either volcanoes that never reached the surface, or truncated ones that sank at a faster rate than coral growth could keep up, in other words, sunken atolls (Hamilton, 1956). Most of these are at a uniform depth of from 700 to 900 fathoms (1260 to 1620 m.), and so are too deep to be used by present-day propagules (dispersal units). When at or near the surface, however, they may have served as stepping-stones as do islands and atolls today.

7. Sea-level fluctuations.

In addition to the rising and sinking of tectonic blocks, the sea level has fluctuated widely in the comparatively recent past. It is the amount of fresh water tied up in glaciers (chiefly the Antarctic and Greenland ice-caps) that controls the sea level. At its maximum 36,000 years ago, the Wisconsin ice sheet lowered the sea level by as much as 460 feet (Haag, 1962, p. 120). This would have been enough to have exposed the shallower banks, such as Ranger Bank off Baja California (67 fathoms) and Hurricane Rock, south-west of Clarion Island (15 fathoms), but not the deeper seamounts.

8. Temperature changes.

The Pleistocene was a period of great temperature fluctuations, particularly on the North American continent, (Hubbs, 1967, p. 338) where the Wisconsin Ice Sheet penetrated the upper Mississippi-Ohio River drainage systems (Broecker, *et al.*, 1960: 441; Hubbs, 1967: 338; Orr, 1967: 318). As the glacier retreated, the resulting outflow of melting ice, pouring into the Gulf of Mexico and thence into the Caribbean, could not have failed to reduce both the temperature and the salinity of the surface waters, with the resulting elimination of stenothermic and stenohaline species, including certain corals and their commensals.

9. Trans-Isthmian connections

The former portals that existed across the present Isthmus of Panama, allowing free oceanic circulation between the western Atlantic and eastern Pacific, and making an island continent of South America, were closed by late Miocene (Durham and Allison, 1960). This set the stage for the extinction of the coral genera Stylophora and Po-cillopora of the family Seriatoporidae (Pocilloporidae), which according to Vaughan (1919, p. 222) have been absent from the West Indian region since Miocene. Had one of the three known portals (Tehuantepec, across Mexico; Panama; Bolivar Trench across Colombia) persisted through Pliocene-Pleistocene, allowing drainage of surface waters of the Gulf of Mexico-Caribbean Sea into the Bay of Panama, these genera might be found in the Caribbean today.

10. Ocean-floor spreading.

This excruciatingly slow process, which has been studied intensively with the newer techniques of echo-sounding, deep-ocean coring, and seismology, appears at first glance to have little bearing on distribution of crabs or corals until one realizes that (a) the continents are moving farther apart, (b) the amount of spread, in the south Pacific at least, coincides almost exactly with the extent of the mid-Pacific oceanic barrier, and (c) that east Asia and west America were much closer to each other in the remote past, when corals, followed by their commensals, began their outward migration from a presumed center of distribution in the East Indian region, not far from the Coral Sea.

E. CONCLUSION

It may be concluded, therefore, that what is known of oceanic currents, larval stages, island stepping-stones, submerged seamounts, sea-level fluctuations, temperature changes, trans-Isthmian connections, and ocean-floor spreading in the eastern tropical Pacific all points to the transport of larval stages of coral-inhabiting decapods over great distances through long periods of time. Their survival in the new environment, a matter of chance with free-living species which must adapt to new conditions by change, is virtually assured for the coral commensal, which finds a ready-made habitat in the coral of its preference, provided the coral arrived there before it.

II. SYSTEMATIC ACCOUNT

A. Subsection HAPALOCARCINIDEA I. Family HAPALOCARCINIDAE

a. Hapalocarcinus marsupialis Stimpson

Hapalocarcinus marsupialis Stimpson, 1859, p. 412 (Hilo, Hawaii). Edmondson, 1923, p. 24 (Palmyra). Schmitt, 1936, p. 34, figs. 36a-f (Port Utria, Columbia). Rathbun, 1937, p. 259, pl. 79, figs. 3-9, text-fig. 46 (Secas Islands, Panama). Garth, 1965, p. 8, figs. 1, 2 (Clipperton).

Distribution. Indian and western Pacific oceans east to Hawaii and Palmyra. Eastern Pacific at Panama and Colombia; Clipperton Island.

Habitat. Pocillopora and other corals, in which it forms galls. Hosts listed by Edmondson (1923) in the central and western Pacific include Seriatopora, Stylophora, Sideropora, and Millepora.

b. Pseudocryptochirus crescentus (Edmondson)

Cryptochirus crescentus Edmondson, 1925, p. 33, text-fig. 6, pls. B, C (Johnston Island).

- *Troglocarcinus (Troglocarcinus) crescentus,* Fize and Serène, 1957, p. 62, text-figs. 10, 11c, 11d, 12b, pl. 3, figs. 4-7, pl. 5, fig. 2, pl. 11, fig. B (Nha-Trang, Viet Nam). Garth, 1965, p. 8, figs. 3-6 (Clipperton Island).
- Pseudocryptochirus crescentus, Serene, 1966, p. 396, Garth and Hopkins, 1968, p. 41 (off El Tule Ranch, 10 mi. E. of Cape San Lucas, Baja California).

Distribution. Western Pacific from Hong Kong, Palao, and Viet Nam to Johnston Island, Line Islands. Eastern Pacific at Clipperton Island and Cape San Lucas, Baja California.

Habitat. Massive corals of the genus *Pavona*, in which it forms crescent-shaped tunnels closed by the anterior portion of the carapace and the meral segments of the first pair of walking legs.

B. Subsection BRACHYGNATHA Superfamily BRACHYRHYNCHA 2. Family XANTHIDAE

a. Domecia hispida Eydoux and Souleyet

Domecia hispida Eydoux and Souleyet, 1844 (or 1845), p. 235 (Sandwich Islands), Finnegan, 1931, p. 647 (Gorgona Island). Crane, 1937, p. 73 (Arena Bank, Gulf of California); 1947, p. 82 (Clarion Island). Garth, 1946, p. 489, pl. 81, fig. 5 (Galapagos Islands); 1948, p. 50 (La Plata Island, Ecuador); 1965, p. 23 (Clipperton Island).

Distribution. Indo-west Pacific from Red Sea to Hawaii. Eastern Pacific from Baja California to Ecuador. Clarion, Cipperton, and Galapagos Islands.

Habitat. The Pocillopora colony.

b. Trapezia digitalis Latreille

- Trapezia digitalis Latreille, 1825, p. 696 (Red Sea). Rathbun, 1930, p. 559, pl. 228, figs. 5, 6 (Socorro, Clarion Islands).
 Schmitt, 1933, p. 22 (Galapagos Islands). Crane, 1937, p. 73 (Arena Bank, Gulf of California); 1947, p. 83. Garth, 1946, p. 493, pl. 81, fig. 6; 1948, p. 51 (La Plata Island, Ecuador). Hertlein and Emerson, 1957, p. 5 (Clipperton Island).
- Trapezia corallina Gerstaecker, 1857, p. 126 (Veragua, Panama).
- Trapezia nigro-fusca Stimpson, 1860, p. 219 (Cape San Lucas, Baja California).
- Trapezia formosa Smith, 1869, p. 286 (Pearl Islands, Bay of Panama).

Distribution. Indo-west Pacific from Red Sea to Hawaii. Eastern Pacific from Gulf of California to Ecuador. Clarion, Socorro, Clipperton, and Galapagos Islands.

Habitat. The Pocillopora colony.

c. Trapezia ferruginea Latreille

Trapezia ferruginea Latreille, 1825, p. 695 (Red Sea).

Trapezia cymodoce ferruginea, Rathbun, 1907, p. 58 (Easter Island); 1930, p. 557, figs. 1, 2 (Clarion Island). Boone, 1927, p. 240 text-fig. 88 (Cocos and Galapagos Islands). Crane, 1937, p. 73 (Arena Bank, Gulf of California); 1947, p. 83, Garth, 1946, p. 491, pl. 81, fig. 4; 1948, p. 51 (La Plata Island, Ecuador). Hertlein and Emerson, 1957, p. 5 (Clipperton Island).

Distribution. Indo-west Pacific from Red Sea to Hawaii. Eastern Pacific from Gulf of California to Ecuador, Clarion, Clipperton, Galapagos, and Easter Island.

Habitat The Pocillopora colony.

d. Trapezia areolata Dana

- *Trapezia areolata* Dana, 1852a, p. 83; 1852b, p. 259; 1855, pl. 15, fig. 8a (Tahiti). Forest and Guinot, 1961, p. 135, fig. 133 (Hikueru).
- Trapezia ferruginea areolata, Ortman, 1897, p. 206, synonymy.

Distribution. From Ceylon and Nicobar Islands to Tahiti and Tuamotu (Hikueru). Easter Island (Medical Expedition to Easter Island, Garth, 1973). *Habitat.* Normally *Pocillopora* coral. METEI specimens were recovered from the stomach of a large starfish (*Leiaster leachii*) that had apparently been feeding on coral.

e. Trapezia danai Ward.

- *Trapezia maculata* Dana, 1852b, p. 256 (part); 1855, pl. 15, fig. 4d (not 4 a-c). Stimpson 1960, p. 219 (?Socorro Island). (Not *Grapsilius maculatus* MacLeay, 1838, p. 67.)
- Trapezia cymodoce maculata, Rathbun, 1930, p. 558, pl. 228, figs. 3, 4 (Not Grapsilius maculatus MacLeay, 1838, p. 67.)
- Trapezia danae Ward, 1939, p. 13, figs. 17, 18. (Name substituted for *T. maculata* Dana, a junior homonym of *T. maculata* (MacLeay).
- Trapezia aff. danai, Serène, 1969, p. 136, figs. 14A, 14 B, 15, 16, 21, 22, 24.

Distribution. This cannot be given with precision. because of confusion over the name "maculata," which has been applied to two different spotted species, the maculata of MacLeay belonging to the T. rufopunctata group (the type, examined by the author, in the MacLeay Museum at the University of Sydney), the maculata of Dana to the cymodoce group of Trapezia. Dana's material from Hawaii and Tahiti probably contained more than one species, fide, Serène (1969, p. 136), who applies Ward's name to one of Dana's Hawaiian specimens (fig. 4d). Ward's material was from Samoa; he failed to distinguish between Dana's Tahitian and Hawaiian specimens. Stimpson's material, purportedly from Socorro Island, but forwarded to him by John Xantus, keeper of the light at Cape San Lucas, more probably came from Hawaii also, as Xantus is not known to have visited the Revilla Gigedo Islands, of which Socorro is one, and no spotted Trapezia has been found in the Eastern Pacific since that time. An exception is Easter Island, where a finely spotted Trapezia, which may be referable to T. danai, was obtained by the University of Concepción Expedition of 1972 (Garth, 1973, p. 321).

Habitat. The Pocillopora colony.

f. Quadrella nitida Smith

Quadrella nitida Smith, 1869, p. 288 (Pearl Islands, Bay of Panama). Rathbun, 1898, p. 590 (off Cape San Lucas, Baja California); 1930, p. 561, pl. 229. Crane, 1937, p. 74 (Arena Bank and Gorda Bank, Gulf of California). Garth, 1946, p. 494, pl. 80, fig. 6 (Galapagos Islands).

Distribution. Eastern Pacific from Gulf of California to Bay of Panama. Galapagos Islands.

Habitat. The gorgonian coral, Muricea miser Verrill (Crane, 1937), in depths of 6-75 fathoms.

g. Maldivia galapagensis Garth

Maldivia galapagensis Garth, 1939, p. 22, pl. 8, figs. 1-6 (Galapagos Islands); 1946, p. 495, pl. 80, fig. 5.

Distribution. Eastern Pacific at Galapagos Islands and Port Parker, Costa Rica (unpublished record).

Habitat. The compact heads of "brain coral" (Pavona sp.) (Garth, 1946).

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