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Biotropica, Vol. 7, No. 1. (Apr., 1975), pp. 12-23.

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Coral-Reef Asteroids of Guam¹

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ABSTRACT

Most coral-reef asteroids of Guam, at least 24 species in total, represent those which are widely distributed in the Indo-West Pacific. The diversity of asteroid fauna in Micronesia and its surrounding region follows a general trend of a faunal center in the rich Indo-Malayan Archipelago area with the number of species diminishing eastward in the scattered and remote oceanic islands. Larval development in many common reef asteroids is oriented toward dispersion by producing planktotrophic and surface-floating larvae which stay in the pelagic environment for three weeks or longer. The major oceanic surface currents flow westward, driven by steady trade winds in the area surrounding Guam and most of the Micronesian Islands. It is argued that local recruitment of asteroid populations might be hazardous under such circumstances where coastal water masses would hardly conserve larval populations inshore. Juvenile populations of reef asteroids have been rarely located in the field, in spite of conspicuous adult populations. Feeding habits, life histories, and other aspects of natural histories of reef asteroids are discussed.

THE CURRENT PROBLEM of *Acanthaster planci* infestations on reef-building corals has called attention to the fact that little knowledge concerning the biology and ecology of coral reefs and their associated organisms has been accumulated to date. Although there are reports on systematic and zoogeographical studies of coral-reef asteroids and other echinoderms in the tropical Indo-West Pacific (see recent monograph by Clark and Rowe 1971), little is known about behavioral aspects of population recruitment or about feeding, growth, predation, and life history.

The problem of *Acanthaster* infestations is essentially a matter of population dynamics. An understanding of the mode of population recruitment of the starfish to the coral-reef environments of oceanic islands is vitally important in evaluating the processes maintaining asteroid populations. The confusion among the many hypotheses which have been developed to explain the causes of *Acanthaster* infestations seems to derive for the most part from lack of knowledge concerning the manner and processes of recruitment to the coral reefs. Thus there are two extreme predictions concerning the infestation: one expects expanding infestations to occur as long as human interference with nature exists (Chesher 1969), and the other suggests that present infestations are episodic phenomena (Walsh *et al.* 1971).

Although arguments about infestations are concentrated only on *Acanthaster planci*, the existence

of many other conspicuous coral-reef asteroids must be considered. In spite of the great diversity of adult structure, habitat, behavior, and population densities, many common asteroids produce larvae with similar structure and behavior (Yamaguchi 1973a). This situation suggests that environmental pressure to reduce larval populations may work in a similar manner among many species, resulting in stereotyped larval forms.

The island of Guam is located in the trade wind zone where steady, continuous winds produce surface currents drifting in one direction for long periods of time over much of the year. Most asteroid larvae, as well as larvae of other shallow-water inhabitants, may be transported by the currents away from the island for a great distance and would be most unlikely to be able to recruit to the mother populations. Many asteroids have a three- to four-week larval life span as plankton. This period is long enough for their wide dispersion and transportation, for example, over the distance from Guam to the Philippines, if given a current velocity of one and a half knots.

Almost nothing is known about water movement in the open ocean nor in the areas near the islands, except for some crude data on prevailing current such as the North Equatorial Current. Eddy formation and movement multiplies problems of understanding larval dispersion. It is difficult to discuss the mode of recruitment and colonization of coastal animals on coral reefs when we lack reliable information on water movement and its effect on the breeding behavior of these animals and on their larval ecology.

¹Supported in part by the Government of Guam *Acanthaster* research appropriation and NSF grant GA39948. Contribution No. 54, University of Guam Marine Laboratory.

GEOGRAPHICAL DISTRIBUTION OF CORAL-REEF ASTEROIDS IN MICRONESIA AND SURROUNDING AREAS

As the name indicates, all the islands in Micronesia are small, and all are scattered in a wide area of the tropical North Pacific Ocean. These islands are surrounded by coral reefs which have many groups of divergent organisms. Although we have some knowledge concerning the systematics of coral-reef animals and their occurrences in certain areas, there is a great gap in our understanding of how such animals maintain their populations on tiny islands, each isolated by wide expanses of ocean. Consideration of the zoogeographical distribution of asteroids, which are one of the most conspicuous animal groups on the reef, may give some clue to the explanation.

This section is an attempt to compile the scattered information on coral-reef asteroids in Micronesia in order to relate this to information about species found on Guam. There are reasonably complete reports on shallow-water asteroids of surrounding areas such as Hawaii (Fisher 1906; Ely 1942), Ogasawara (Hayashi 1938a; Oishi 1970), Okinawa (Djakonov 1930; Hayashi 1938b), and the Philippines (Fisher 1919; Domantay and Roxas 1938; A. H. Clark 1949); but the Micronesian asteroid fauna is poorly known. Collections made by the "Albatross" included a few species of shallow-water asteroids from Ponape and Jaluit (Ludwig 1905), but most information on Micronesian coral-reef asteroids is rather recent and incomplete. Hayashi (1938c) reported on the asteroid fauna of Palau with some additional data from other Caroline Islands. A. H. Clark (1952, 1954) reported on the collection of asteroids in the U.S. National Museum from the Marshalls and some other areas, including the Marianas. Cloud (1959) recorded asteroid species in his list of shoal-water fauna and flora found in Saipan.

A number of asteroid specimens collected by students and faculty were deposited at the University of Guam prior to the collection made by myself. They included a few species such as *Astropecten polyacanthus* which I have yet to find. During 1972 and 1973, I made nearly 40 field surveys searching for asteroids in various parts of Guam. The starfish control team, which was in charge of monitoring the population of *Acanthaster planci* around Guam, and other members of the Marine Laboratory contributed many specimens of rare species. The specimens collected from the shallow

water of Guam number over 300 and consist of at least 24 species. This may represent the most extensive collection of asteroids known from Micronesia to date.

In addition to the above, there are 28 specimens collected from the northern Marianas in the collection of the University of Guam Marine Laboratory. They do not contain any species in addition to those of Guam. At present (July 1974), the asteroid fauna of the Eastern Carolines is the least known in Micronesia. Dr. K. Hayashi of the Marine Parks Center of Japan kindly collected specimens of *Echinaster luzonicus* from Truk on his trip and contributed a new locality record for the species.

Table 1 is the summary of the records of coral-reef asteroids in Micronesia as pooled for four island groups (Marianas, W. Carolines, E. Carolines, and Marshalls), as well as records from surrounding areas. Data from the Western Carolines are mostly from Palau; and the Eastern Carolines, from Truk and Ponape. The records for the Marshalls were mostly from northern atolls such as Eniwetok and Bikini. The "Tanager" Expedition collected some asteroids from the isolated islands of Johnston, Wake, and Palmyra (Fisher 1925). Marsh (1974) reported on asteroids from the Line Islands along with those from S.E. Polynesia. These records are included in the last column of the table.

The asteroid species in table 1 are divided into three groups. The first group consists of sand-bottom inhabitants, which were not searched for extensively. Only one species was recorded on Guam. The second group includes those commonly found on Guam and recorded as common in most areas. The third group comprises less common species. All species with single locality records have been excluded, and those which have been recorded from the Philippines but not from the remaining areas in the table are also excluded; they include species of *Stellaster*, *Halityle*, *Asterodiscus*, *Anthenea*, *Bunaster*, *Poraster*, *Iconaster*, and *Tamaria*, as well as certain species of *Astropecten*, *Archaster*, *Fromia*, *Nardoa*, and *Ophiaster*. It is obvious that most of the asteroids of the tropical oceanic islands of the North Pacific have also been recorded from the Philippines. However, several rather rare species such as *Dactylosaster cylindricus* and *Neoferdina cumingi*, found in oceanic islands, were not recorded from the Philippines.

Uniformity of distribution in the marine inshore fauna of the tropical Pacific has often been noted (e.g. Wiens 1962), although there are local differences in composition and relative abundance reflecting variations in environments such as habitat

complexity (Kohn 1967). In contrast to the uniform asteroid fauna in the tropical Pacific, it is a striking fact that New Zealand waters carry so many endemic (26 out of 30) species of asteroids and that the fauna has only little in common with that of Australian asteroids (H. L. Clark 1946). The Tasman Sea which separates New Zealand from Australia is similar in expanse to the Philippine Sea which divides Guam and the Philippines.

H. L. Clark (1921) considered the geographical distribution of echinoderms in the tropical Pacific, with emphasis on the fauna of Torres Strait, North-

ern Australia. His data on asteroids clearly indicated that the pattern of eastward attenuation of species in the southern hemisphere is similar to the pattern in the northern hemisphere. A recent consideration on zoogeography of Polynesian asterozoans confirms the eastward attenuation in both asteroids and ophiuroids (Devaney 1973).

It seems that the asteroid species in the tropical Pacific in general extended their distribution eastward from the continental area to oceanic islands, with a reduction in the number of species away from the rich, divergent fauna of the East Indies, the

TABLE 1. Geographical distribution of shallow-water asteroids in Micronesia and surrounding area.^a

Genus and species ^b	Philippines	Ryukyu	Ogasawara	W. Carolines	Marianas	E. Carolines	Marshalls	Gilberts	Hawaii	Other N. Pacific Islands
<i>Luidia aspera</i>	X								X	
<i>L. savignyi</i>	X						X			
<i>Astropecten polyacanthus</i>	X				X		X		X	
<i>Archaster typicus</i>	X	X		X					X	
<i>Culcita novaeguineae</i>	X	X		X	X	X	X	X	X	J ^a
<i>Linckia laevigata</i>	X	X	X	X	X	X	X	X		
<i>L. multiflora</i>	X	X	X	X	X	X	X	X	X	JWPF
<i>Ophidiaster granifer</i>	X	X		X	X	X	X			
<i>Acanthaster planci</i>	X	X	X	X	X	X	X	X	X	JF
<i>Echinaster luzonicus</i>	X	X	X	X	X	X	X	X		P
<i>Choriaster granulatus</i>	X	X		X	X					
<i>Pentaceraster regulus</i>	X	X								
<i>Pentaster obtusatus</i>	X	X								
<i>Protoreaster nodosus</i>	X	X			?					
<i>Linckia guildingi (diplax)^c</i>	X	X	X	(X)	X		X		X	
<i>Ophidiaster squameus (pustulatus)^c</i>	X	(X)			X		X		X	
<i>O. loroli (cribrarius)^c</i>		(X)	(X)				X		X	WP
<i>Fromia monilis</i>	X	X		X		X		X		
<i>F. indica</i>	X	X	X	X						
<i>F. milleporella</i>	X	X	X		X					P
<i>F. hemioplata</i>	X				X		X			
<i>F. pacifica</i>	?						X		X	
<i>F. hadracantha</i>	X	X								
<i>Dactylosaster cylindricus</i>					X		X		X	
<i>Neoferdina cumingi (cancellata)^c</i>					X		(X)			W
<i>Gomophia egyptiaca</i>					X			X	?	
<i>Nardoa tuberculata</i>	X	X		X						
<i>N. tumulosa (frianti)^c</i>	X	X	(X)	X						
<i>Leiaster leachi (speciosus)^c</i>	(X)	X			X				X	
<i>Asteropsis carinifera</i>	X	X	X	X	X				X	C
<i>Asterina anomala (cephus)^c</i>	(X)	X			X		(X)	(X)	X	W
<i>A. coronata</i>	X	X				X	X			P
<i>Patiriella exigua</i>	X	X		X						
<i>Mithrodia clavigera</i>	X	X		X	X					
<i>M. fisberi</i>	X								X	J
<i>Coscinasterias acutispina</i>		X	X						X	

^a Ryukyu: Amami, Okinawa, and Yaeyama groups; W. Carolines: mostly Palau; Marianas: Guam and Saipan; E. Carolines: Truk and Ponape; Marshalls: Eniwetok and Bikini; Gilberts: Onotoa; Hawaii: all Hawaii group; Other N. Pacific Islands: (J: Johnston, W: Wake, P: Palmyra, C: Christmas, F: Fanning).

^b The first group includes sand-bottom inhabitants, the second common species of Guam, and the third less common species. All species with single locality records have been excluded from this list.

^c Species names with parenthesis indicate possible synonym or allopatric related species.

Philippines, and North Australia. It is well demonstrated that the number of genera of reef-building corals decreases radially in the Pacific away from the rich Indo-Malayan region (Wells 1954). Rosewater (1965) discussed the geographic distribution of the giant clams, *Tridacnidae*, which are confined to the Indo-Pacific. He postulated the specific variation in the ranges of distribution to be related to length of larval life. It is clear from his maps of the geographical distribution of the six extant species that the giant clams have centers of population around the Philippines, East Indies, New Guinea, and Western Carolines in Micronesia, with a reduction of species radially to the more remote oceanic islands.

It is difficult to discuss the negative records because the supposed absence or presence of less common species reflects primarily the extent of search efforts in different areas. There is also a problem in the synonymy of morphologically variable species based on only occasional specimens. Nevertheless, there are some peculiarities in the faunal composition of the Palauan asteroids as compared to the rest of Micronesia, Hawaii, and the Gilberts. The waters of Palau contain some species which seemingly have not extended their range eastward, for example, if *Gomophia* is not congeneric with *Nardoa*, no species of *Nardoa* have been recorded east of Palau in Micronesia, Hawaii, or the Gilberts. Equally unexpectedly, *Gomophia*, *Neoferdina*, and *Dactylosaster* were not recorded from Palau (Hayashi 1938c) but are recorded from islands further east. These three have also not been recorded from Okinawa, Ogasawara, and the Philippines. In relation to the above, the occurrence of *Nardoa* in the Ogasawara Islands (Hayashi 1938a; Ooishi 1970) is interesting and noteworthy. Some species of *Fromia* might show a similar pattern of allopatry to the above-mentioned genera, but the problem of synonyms in this morphologically variable genus prohibits further discussion.

The two species of Oreasteridae, *Choriaster granulatus* and *Protoreaster nodosus*, are both conspicuous and occur in fully exposed habitats. Their presumed absence in Hawaii may be real, since the marine fauna of the area has been studied extensively for a long period. It is not clear whether or not the two are distributed eastward beyond Guam. A systematic search for asteroids in the Eastern Carolines is desirable in order to answer this question. The record of *Protoreaster* from Guam by A. H. Clark (1954) may be questionable, since specimens of this species have not been collected by anyone since the original six specimens were collected in

1945. However, I consider it likely that *Protoreaster* once existed on the reefs of Guam because the site and date of collection, as well as the names of collectors, were given.

Coscinasterias acutispina is one of the few representatives of the Order Forcipulata in warm water, while many species of the order dominate the asteroid fauna in different parts of the cold-water regions. This species is very common along the southern coast of Japan, and its distribution extends south to the Amami group and the Ogasawara group (Hayashi 1938a). The occurrence of *Coscinasterias acutispina* is said to represent the Japanese element in the Hawaiian fauna (Fisher 1925). The recently discovered subtropical counter current at about 20°N (Yoshida 1970) may explain the occurrence of Japanese elements in the Hawaii fauna.

LARVAL DEVELOPMENT AND TRANSPORTATION IN RELATION TO GEOGRAPHICAL DISTRIBUTION

It is evident from table 1 that the asteroid fauna of the Marianas (Guam) is very similar to that of other oceanic islands in the tropical Pacific. The fauna of the Marshalls especially has a close resemblance, in spite of remarkable differences in the geomorphology between the two island groups. The Marianas consist of high islands with rather poorly developed fringing reefs, as contrasted with the atolls of the Marshalls. In other words, many of the asteroid species of oceanic islands are very widely distributed in the tropical Pacific. This situation may be because of their successful larval transportation throughout the area as a whole. Although Thorson (1961) indicated that there is little possibility of trans-oceanic larval transportation in most marine benthic invertebrates, insular larval transportation of reef asteroids may occur among the scattered oceanic islands in Oceania. Scheltema (1968, 1971) gave some direct evidence of trans-oceanic larval dispersal in tropical gastropods and other invertebrates and related this to the oceanic currents. On the other hand, Briggs (1967) expressed the opinion that biological competition is a more important factor in the distribution of tropical shore animals than the direction of major oceanic currents.

The surface oceanic current system in Micronesia and the surrounding area consists of the North Equatorial Current and the Equatorial Counter Current (Wiens 1962). The western part of the area may be strongly affected by monsoon drift, and the peculiar asteroid fauna of Palau may be related to the eastward drift current, as well as to its proximity to the continent.

Although there are counter currents moving eastward near the equator in the surface current system of the tropical Pacific, the predominance of trade winds and the related North Pacific Equatorial Current may have a strong adverse effect on local recruitment of coral-reef asteroids in many islands of Micronesia, as well as in range extension of animals eastward from the western faunal centers. Guam and other islands in the Marianas may be most affected by this because of their location in a region where the trade wind is fairly constant during long periods of the year and because the topography of the reefs results in their direct exposure to open ocean currents. Nevertheless, there are a number of species which colonize the shallow water of these islands, i.e., the second group of asteroids in table 1.

Acanthaster planci has already shown mass recruitment in most of the southern islands in the Marianas. Saipan, located about 200 km north of Guam and separated from it by a depth of about 400 fathoms, had a large number of *Acanthaster* at the same time Guam did (Goreau *et al.* 1972). It is unlikely that adult starfish could migrate from one of these two islands to the other; primarily because of the distance, it takes over one year for an adult starfish to travel 200 km at the rate of 20 m/hr, and also because of the cold temperature of the deep water (below 10°C at 200 fathoms) which separates the islands. The starfish infestations in Saipan, Tinian, Aguijun, Rota, and Guam might have been caused by massive recruitment of the starfish on each island independently, although there remains some possibility of adult migration between the first three islands, which are quite close to one another.

The atolls in Micronesia so far surveyed have been reported not to be infested by *Acanthaster* (Marsh and Tsuda 1973). It is known that surface water in atoll lagoons, which is usually driven by the trade winds, drifts steadily to leeward and flows out through western channels (Johnson 1954). Since larval *Acanthaster* as well as larvae of other species swim to the surface, the environments in atolls are presumably unfavorable for their local recruitment. Size and topography of islands may have a strong influence on the mode of population recruitment for many organisms because water movement around islands is modified greatly by such local factors.

Mortensen (1938) remarked that larvae of *Pentaceraster mammillatus* were active swimmers but did not stay near the surface, while the rest of the asteroid species studied did. This *Pentaceraster* is distributed only along the continental region of the

western Indian Ocean (Clark and Rowe 1971). A combination of oceanic current and larval behavior may be the major influence on the geographical distribution of this asteroid and of many other species.

Sixteen species of the 36 listed in table 1 have been studied as larval forms. There are three types of larval development among the species of shallow-water asteroids in the tropical Indo-Pacific. Most sand-dwelling species (*Luidia* and *Astropecten*) produce planktotrophic bipinnaria larvae which metamorphose without forming attachment organs, and so lack the brachiolaria stage. However, the sand-dwelling species *Archaster typicus* produces brachiolariae, and attachment of larvae to the substrate was observed in this species (Mortensen 1931).

Larval development in the reef-dwellers may be divided into two distinctly different types, planktotrophic and lecithotrophic. Two species of Oreasteridae (*Culcita* and *Choriaster*) produce larvae of the plankton-feeding (planktotrophic) type, and the others such as *Protoreaster* and *Pentaceraster* may do the same. Larvae of *Linckia*, *Asteropsis*, *Acanthaster*, *Leiaster*, *Mithrobia*, and *Coscinasterias* are all known to be planktotrophic (Mortensen 1921, 1931, 1937, 1938; Komatsu 1973; Yamaguchi 1973a and unpublished). Many of the other species in the table may produce nonfeeding (lecithotrophic) larvae with dark pigmentation and strong buoyancy because of the yolk. These forms have a reduced stage equivalent to the brachiolaria with attachment organs. This condition has been confirmed for *Patiriella* (Mortensen 1921), *Gomophia* (Yamaguchi 1974a), and *Ophidiaster granifer* (personal observation). *Fromia ghardagana* produced "perfectly intransparent red lump" embryos (Mortensen 1938). Species of *Nardoia* are likely to produce lecithotrophic larvae, since the allied species *Certonardoia semiregularis*, which is common in southern Japan, does so (Hayashi and Komatsu 1971). *Echinaster purpureus*, closely related to *E. luzonicus*, produces lecithotrophic larvae (Mortensen 1938). The number of species with lecithotrophic larval development may be similar to that with planktotrophic larval development. However, most of the species with lecithotrophic development, except *Ophidiaster granifer* and *Echinaster luzonicus*, have not been abundantly recorded from any oceanic island locality. On the contrary, they are considered rare and are usually represented by only a few specimens (A. H. Clark 1952, 1954).

Some species of asteroids are known to reproduce asexually by autotomy of rays, for example *Linckia multifora*, *Linckia guildingi*, *Ophidiaster cribrarius*, and *Echinaster luzonicus*, or by fission of the total

body, as in *Asterina anomala* and *Coscinasterias acutispina*. This circumstance could be responsible for the abundance of these species in certain localized areas. The hazards of recruitment by sexual reproduction would be compensated by the maintenance of populations by asexual reproduction.

NATURAL HISTORY OF CORAL-REEF ASTEROIDS OF GUAM

There is no substantial field study on the feeding, behavior, and habitat requirements of coral-reef asteroids except for some work on *Acanthaster planci* (Goreau 1964). Goreau *et al.* (1972) remarked that *Culcita novaeguineae* is another coral predator. I witnessed *Asterina* sp. in aggregation feeding on the coral *Acropora echinata* at Palau (at about 10 meters depth on a patch reef located north of Koror Island in February 1971).

The question of the nutrition source for *Echinaster luzonicus* (Echinasteridae) and many of the species of Ophidiasteridae, which includes *Linckia*, *Ophidiaster*, and others, is very puzzling. They have often been observed in the field everting their stomachs on the substrate. However, no special food organisms were apparent to the naked eye. James and Pearse (1969) suggested that *Linckia multifora* might be a suspension feeder, although they noted that its stomach everted. This starfish is unlikely to be a suspension feeder because, in the observations made in the field, the stomach was always in close contact with the substrate and sometimes a feeding mark was recognizable on the spot where the stomach had been everted. In laboratory aquaria such starfish appeared to be digesting microscopic organisms or algae growing on the surfaces of substrates. These asteroids may be herbivores or detritivores similar to the early juvenile stage of *Acanthaster* (Yamaguchi 1973a) and possibly also the early juvenile of *Culcita*, which feeds on encrusting algae, especially coralline algae and epibenthic diatoms.

Choriaster granulatus, *Linckia guildingi*, and *Asteropsis carinifera* in holding aquaria feed on dead fish and other animal tissues. Thus they might be regarded as scavengers. Kohn (1959) reported that in an aquarium in Hawaii *Asterope* (= *Asteropsis*) fed on cone shells, but only occasionally. This practice might have been a case of scavenging dead or weak animals instead of devouring healthy, living gastropods.

The paucity of carnivorous species among coral-reef asteroids is in marked contrast to their abundance in colder waters. In aquaria, *Fromia hemioplata*

fed on a particular encrusting sponge, and *Gomophia egyptiaca* fed on some of the solitary ascidians that were offered and on the sponges *Tethya* spp. and *Cinachyra australiensis*. Both species of asteroid appeared to have marked feeding preferences for a limited number of prey species.

More than 12 young *Asterina anomala* were found under rocks encrusted with ascidians, sponges, and other organisms from the reef flat of Pago Bay, Guam, in October 1972. A species of didemnid ascidian was under attack by these starfish when the rock and starfish were collected and placed in an aquarium together. Later it was noted that all the didemnid ascidian colonies had been grazed upon, but none of the botryllid ascidians on the same rock had been attacked by the starfish. A selecting feeding response in *Acanthaster* to various scleractinian corals has been noted in the field (Goreau 1964; Pearson and Endean 1969; Branham *et al.* 1971) and in the laboratory (Brauer *et al.* 1970). It will be interesting to investigate more fully the mechanism of selective feeding discrimination among closely related prey animals by the starfish predators.

Some large species of conspicuous asteroids usually stay on fully exposed reef-flats or reef-terraces. *Culcita*, *Choriaster*, *Linckia*, and other exposed species are equipped with a thick and heavily calcified skeleton. Cryptic behavior of juveniles of these species, as well as that of soft-bodied species and other smaller species, may reflect heavy predation pressure, presumably by fish. Many specimens of asteroids collected from the reef in Guam showed marks of injuries and subsequent regeneration. On the other hand, the small and soft-bodied *Echinaster luzonicus* is often exposed on the reef-flat because its feeding habits are similar to those of *Linckia laevigata*. However, *Echinaster* occurs only in rather shallow, exposed parts of the reef-flat in Guam which may be relatively free from invasions by large fishes. *Echinaster* may, on the other hand, contain a strong repellent substance or toxin in its body as a protective device against predators (see Feder and Christensen 1966).

Juvenile development and morphological changes in *Acanthaster planci* were described from cultured post-metamorphic juveniles. Five-armed newly metamorphosed juvenile *Acanthaster* grew to about 8 mm in total diameter in four months, adding a new ray at about 9- to 10-day intervals until the total number (16 to 18) in normal individuals was reached. Attainment of adult external structures coincided with the transition from feeding on encrusting algae to feeding on corals (Yamaguchi 1973a). One juvenile *Culcita novaeguineae* was

kept in an aquarium for one year after its metamorphosis from the brachiolaria stage. It reached about 7 mm in diameter during that period and was then preserved. This specimen may have consumed the algal substrate as did the early juveniles of *Acanthaster*. The smallest field specimen of *Culcita* found on Guam was about 8 mm in diameter. The morphological changes in juvenile *Culcita* are very remarkable (figs. 1 to 6), and juvenile specimens have been described under different names. For example, Gray gave the names *Hosia spinulosa*, *Goniaster sebae*, and *Randasia granulata* to juvenile *Culcita* (in H. L. Clark 1921). Thus, diversity of structures in these common reef asteroids is established during the course of juvenile development after the completion of similar larval development and the formation of conventional five-armed juveniles just after metamorphosis.

Because of the difficulty in finding small juveniles in the field (Yamaguchi 1973b), it is almost impossible to discuss where settlement of pelagic larvae takes place and the subsequent migration of juveniles occurs. Observation of larvae and early juveniles of *Acanthaster*, *Culcita*, and *Linckia* in the laboratory, combined with observations on many other species by Mortensen (1931, 1937, and 1938), suggests the following pattern. Larvae of coral-reef asteroids in general (excluding sand-bottom species) swim or float close to the surface until metamorphosis, then they may settle on the shallow bottom of the coral reefs when they come in contact with the substrate. The water turbulence in the area may control the final settling site for individual larvae.

The asteroid larvae may be consumed by a spectrum of predators consisting of both pelagic and benthic animals. The fish *Abudefduf curacao* has been reported to feed on the newly released eggs of *Acanthaster* in the field while other fishes ignored the eggs (Pearson and Endean 1969). The reef coral *Pocillopora damicornis* has been observed feeding on larvae of *Acanthaster*, *Culcita*, and *Linckia*, while some planktonic carnivores did not feed on larvae of *Linckia* (Yamaguchi 1973a). Predatory animals may show selective feeding on planktonic prey because of differences in prey size, degree of transparency, and swimming habits. Larvae of asteroids are, in the planktotrophic type, quite transparent and swim steadily, using cilia, whereas many planktonic crustaceans are less transparent and swim in jerky movements caused by use of the muscular system. Planktonic carnivores attack (e.g. *Sagitta*) or trap (e.g. comb-jellies) their prey.

Preliminary observations on the predation of

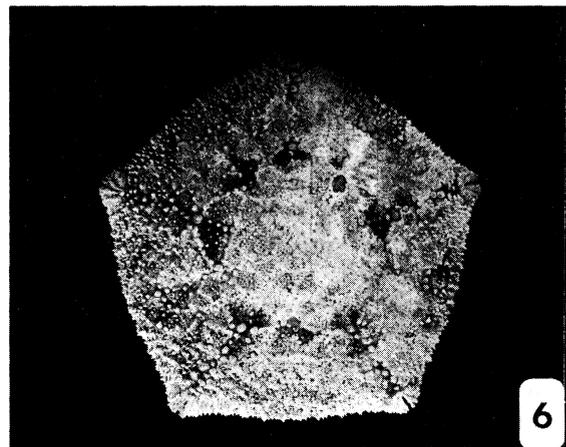
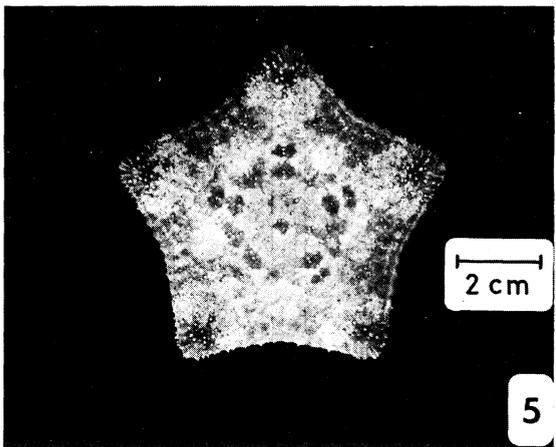
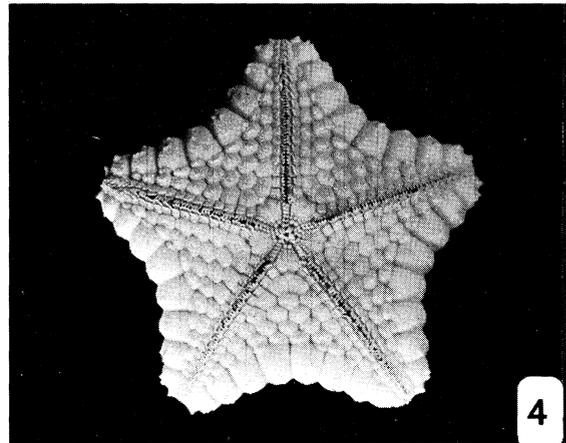
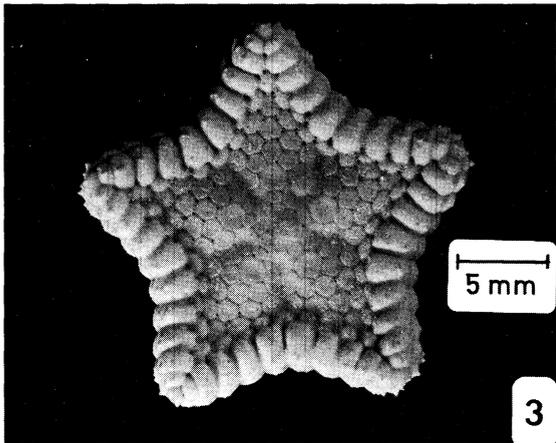
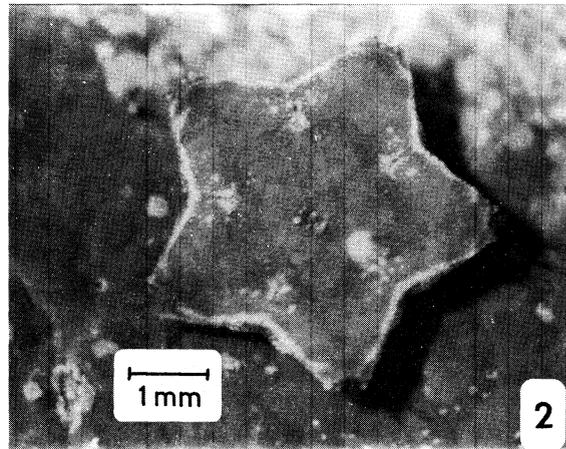
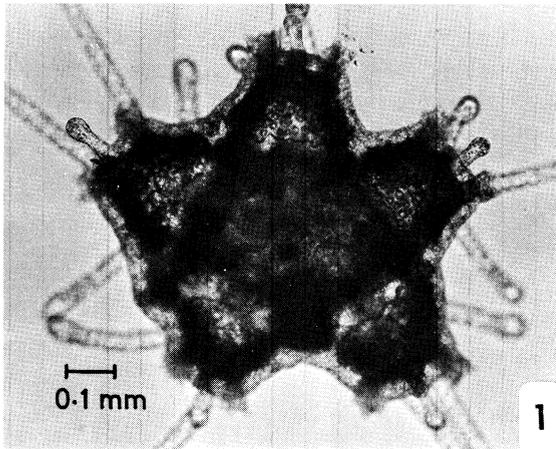
some asteroid larvae by plankton-feeding fish indicated that asteroid larvae in general might contain a chemical repellent substance. Of about 10 fish tested, including several species of *Abudefduf*, all showed a distinct feeding avoidance of any tested asteroid larvae upon visual recognition. Some starved fish expelled larvae immediately after touching or swallowing them. Although several workers have assumed that larvae of *Acanthaster* might be consumed in large numbers by planktonic carnivores (Vine 1970; Randall 1972), asteroid larvae in general, including *Acanthaster*, seemed to be free from many potential predators, such as fishes and perhaps medusae, in the open sea.

The feeding behavior of carnivorous plankters has been studied to consider their potential predation of fish larvae (e.g. Reeve 1964; Fraser 1969; Greve 1970). These studies indicated that predator-prey relationships are often species specific in pelagic communities. The loss of larval populations of asteroids due to dispersal rather than predation should receive more attention; an example of loss through dispersal in gastropod larvae has been presented by Robertson (1964).

A high mortality rate has been observed among metamorphosing larval asteroids at the time of settling on the substratum. Predation by small benthic animals was suggested as one of the possible causes (Yamaguchi 1973a). However, the identification of the predators which might be responsible for the loss of asteroid larvae was not determined.

Juveniles just after metamorphosis are about 0.5 mm in total diameter in species which produce planktotrophic larvae. They may start their well-concealed life on reef substrates where coralline algae encrustation is predominant. We have no data on predation in the natural habitat, but there are many potential predators, such as echinoids, polyclads, and crustaceans. I have noticed an absence of asteroid juveniles on substrates which are colonized by the grazing echinoids *Echinometra* and *Echinothrix*. The growth of juveniles, as defined by the absolute increment of total size, is very slow in the early stages; but exponential growth results in a relatively short duration for the rapidly growing advanced juvenile stage (see e.g. Yamaguchi 1974b, for growth of *Acanthaster* juveniles).

Table 2 summarizes the foregoing account on the coral-reef asteroids of Guam. There are many gaps to be filled by future studies. Feeding of coral-reef asteroids should be emphasized in such future studies, because it is apparently different from that of cold-water asteroids in general. The remarkable morphological and behavioral changes which occur



FIGURES 1-6. Transformation of juvenile *Calcita novaeguineae*. Figure 1: One-week-old juvenile after metamorphosis, aboral surface. Figure 2: 4.5-month-old juvenile, aboral surface. Figure 3 and 4: Small field specimen, aboral and oral surface, respectively. Figure 5: Advanced juvenile, aboral surface. Figure 6: Young post-transformation stage, aboral surface, ca. 9 cm across. Note: Figures 1 and 2 are photomicrographs of live specimens which were raised in the laboratory. Figures 3 through 6 illustrate dried field specimens.

in some conspicuous asteroids during the juvenile to adult transformation stages deserve more careful examination, since such changes may indicate adaptive

evolution in these extremely divergent and specialized species inhabiting the coral-reef environments.

TABLE 2. Summary of coral-reef asteroids of Guam.

Family, genus and species	Habitats and ¹ Abundance		Type of Feeding ³					Type of ⁴ Larval Develop- ment	Type of ⁵ Asexual Repro- duction	Maximum ⁶ Size for Guam Specimen (mm)	Previous ⁷ Records from Guam (Author)
	Reef flat and Lagoon	Sea- ward reef	Habits ²	Carni- vorous on Sessile Animals	Scaveng- ing on Corpses	Sub- strate Feeding on Algae and Microbes	+				
Astropectinidae											
<i>Astropecten polyacanthus</i>	VR	—	Cryp. ?	—	—	—	Pk	—	85		
Oreasteridae											
<i>Choriaster granulatus</i>	VR	R	Expo.	—	+	+?	P	—	115		
<i>Botbriaster primigenius</i> ^a	VR	VR	Cryp.	—	+	—	—	—	22		
<i>Calcita novaeaguineae</i>	C	C	Expo.	+ ^f	—	+	P	—	110	Clark	
<i>Protoreaster nodosus</i>	? ^e	—	Expo.	—	—	+	—	—	—	Clark	
Ophidiasteridae											
<i>Cistina columbiae</i>	VR	VR	Cryp.	—	—	+?	—	—	38		
<i>Dactylosaster cylindricus</i>	VR	—	Cryp.	—	—	+?	—	—	21		
<i>Fromia hemiopl</i>	R	R	Cryp.	+ ^g	—	+	—	—	43		
<i>Fromia</i> sp.	VR	—	—	—	—	—	—	—	28		
<i>Gomophia egyptiaca</i>	R	R	Cryp.	+ ^h	+	+	L	—	60		
<i>Leiaster leachi</i> ^b	R	R	Cryp.	—	—	—	P ⁱ	—	255		
<i>Linckia guildingi</i>	VR	—	Cryp.	—	+	+?	—	A	130		
<i>Linckia pacifica</i> ^c	VR	R	Expo.	—	—	+?	P	—	320		
<i>Linckia laevigata</i>	VC	VR	Expo.	—	+	+	P	—	140	Fisher Clark Fisher	
<i>Linckia multifora</i>	VC	C	Cryp.	—	—	+	Pk	A	45		
<i>Linckia</i> sp.	R	C	Expo.	—	—	+	P	—	240		
<i>Neoferdina cumingi</i>	—	VR	Cryp.	—	—	+	—	—	24		
<i>Ophidiaster granifer</i>	C	—	Cryp.	+? ⁱ	—	+	L	—	41		
<i>Ophidiaster robillardi</i> ^d	R	—	Cryp.	—	—	+	—	A	29		
<i>Ophidiaster squameus</i>	VR	VR	Cryp.	—	—	+	P	—	36	Clark ^m	
Asteropidae											
<i>Asteropsis carinifera</i>	VR	—	Cryp.	—	+	—	Pk	—	75	Clark	
Asterinidae											
<i>Asterina anomala</i>	R	—	Cryp.	+ ^j	—	+	—	F	8		
<i>Asterina</i> sp.	VR	—	Cryp.	+ ^j	—	+	—	—	9		
Acanthasteridae											
<i>Acanthaster planci</i>	R	C	Cryp.	+ ^f	—	+	P	—	250		
Mithrodiidae											
<i>Mithrodia clavigera</i>	R	VR	Cryp.	—	—	—	P	—	250		
Echinasteridae											
<i>Echinaster luzonicus</i>	R	VR	Expo.	—	—	+	—	A	40		

¹ Animals are not uniformly distributed around the island, and their relative abundance is assessed as follows: VC—Very Common, more than 10 individuals could be collected at a given habitat during one-hour search; C—Common, 1 to 10 individuals per one-hour search; R—Rare, specimens are only occasionally encountered in field trips; VR—Very Rare, only a single or a few specimens have been collected. Some rare species appear to make occasional small aggregations at unexpected sites. Negative (—) mark indicates absence of record.

² Cryp.—Cryptic in normal habits during daylight, active only at night; Expo—Exposed on open substrates, although some may be cryptic in habit.

³ There is no known molluscivorous asteroid in this list. Positive (+) mark indicates that feeding was observed either in the laboratory or in the field. Scavenging on dead fish or other animal tissues was observed only in the laboratory. Negative (—) mark indicates that the feeding type was not observed. There is a possibility that some asteroids feed on suspended organic matter by using mucus-ciliary feeding.

⁴ P—Planktotrophic larval development; L—Lecithotrophic development. Negative (—) mark indicates that the larval development of the species has not been studied.

⁵ A—Autotomous asexual reproduction, producing comets; F—Fissiparous asexual reproduction by fission through the disc. Negative (—) mark indicates that there is no evidence of asexual reproduction. Although some species (e.g. *Leiaster*) often autotomize their arm(s), such cast-off arm(s) do not form comets and eventually disintegrate.

- ⁶ Length from the center of disc to arm-tip (shortest arm radius in mm), not for the entire ambulacral groove length.
- ⁷ Clark, A. H. (1954); Fisher, W. K. (1919).
- ^a I suspect that this species represents a juvenile form of *Choriaster*.
- ^b This species includes *Leiaster speciosus* and possibly *L. brevispinus*, both of which I believe to be synonymous with *L. leachi*.
- ^c Fisher (1919) synonymized this species with *L. guildingi*, as well as did the later authors. There is a possibility that *L. pacifica* is an adult form of *L. guildingi*, but I do not have any evidence to prove such at this time. Ely (1942) and Hayashi (1938b) referred to this form as *L. guildingi* from Hawaii and Japan, respectively. *Linckia diplax* from Palau (Hayashi, 1938c) is probably identical to *L. guildingi* from Guam, the latter of which has been compared with the type specimen in the British Museum (Nat. Hist.) by Miss A. M. Clark.
- ^d I identified this species as *O. lorioli* (Yamaguchi 1973b), but Mrs. L. M. Marsh (W. Australian Museum) showed that it should be identified as *O. robillardi*, known previously only from the Indian Ocean.
- ^e *Protoreaster nodosus* has not been collected from any likely habitats, including the site where the old specimens were collected, in recent years. Six specimens were collected by two persons on Guam in 1945 (A. H. Clark 1954). I suspect that this species is now extinct on Guam.
- ^f *Calcia* and *Acanthaster* normally feed on corals. Both species will feed on echinoids, such as *Echinometra* in the laboratory, but it is doubtful that they do in the field.
- ^g *Fromia hemiopl*a feed only on a particular kind of encrusting sponge (not identified) from among many different sponges and other sessile animals tested.
- ^h *Gomophia* feed on soft-bodied solitary ascidians and sponges (*Tethya* spp. and *Cinachyra australiensis*) but not on compound ascidians, hard-shelled solitary ascidians, or sponges other than the above two genera, as far as is tested.
- ⁱ I witnessed several individuals of *Ophidiaster granifer* with their stomachs everted on encrusting sponges in the field, but this observation is not yet confirmed in the laboratory.
- ^j The two species of *Asterina* attack live coral polyps, compound ascidians, and other sessile animals but only occasionally; normally feeding on algal substrates.
- ^k Studied by Mortensen (1937 and 1938) for the Red Sea specimens.
- ^l Early development reported by Komatsu (1973) for Japanese specimens.
- ^m A. H. Clark (1954) recorded this species as *O. pustulatus*.

ACKNOWLEDGEMENTS

I thank the staff of the Marine Laboratory, University of Guam, for its assistance in my research and in the preparation of this manuscript. Miss A. M. Clark of the British Museum (Natural History) has continuously encouraged my

work, and her assistance in identification of asteroid specimens was most helpful. Appreciation is also due to Dr. D. M. Devaney of the B. P. Bishop Museum, Dr. M. E. Downey of the Smithsonian Institution, and Mrs. L. M. Marsh of the Western Australian Museum for enabling me to examine asteroid specimens housed in these Museums.

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