

The Shallow-Water Crinoid Fauna of Kwajalein Atoll, Marshall Islands: Ecological Observations, Interatoll Comparisons, and Zoogeographic Affinities¹

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ABSTRACT: Twelve species of comatulid crinoids in three families were found to inhabit reefs at Kwajalein Atoll during surveys conducted both day and night by divers using scuba gear. Eleven of the species represent new records for the atoll, and five are new for the Marshall Islands. A systematic résumé of each species is presented, including observations on diel activity patterns, degree of exposure when active, and current requirements deduced from local distributions. More than half of the species were strictly nocturnal. Densities of nocturnal populations were much higher than those typically observed during the day. Occurrence and distribution of crinoids about the atoll appeared to be influenced by prevailing currents. Some species, of predominantly cryptic and semicryptic habit by day, occurred at sites both with and without strong currents. While these species were able to survive in habitats where currents prevailed, they appeared not to require strong current flow. In contrast, the remaining species, predominantly large, fully exposed comasterids, were true rheophiles; these were found on seaward reefs and only on lagoon reefs in close proximity to tidal passes. Comparison of crinoid records between atolls in the Marshall Islands shows Kwajalein to have the highest diversity, although current disparities between atolls in the number of species recorded undoubtedly reflect to some extent differences in sampling effort and methods. Based on pooled records, a total of 14 shallow-water crinoid species is known for the Marshall Islands, compared with 21 for the Palau Archipelago and 55 for the Philippines. The Marshall Islands comatulid fauna is predominantly an attenuated western Pacific fauna, dominated by widely distributed members of the family Comasteridae. A field identification key for crinoids of the Marshall Islands is provided.

OUR KNOWLEDGE of the occurrence and distribution of shallow-water crinoids throughout the Indo-West Pacific is still very limited, due in part to the vastness of the region and the remoteness of many of its island groups. The crinoid fauna of Palau, in the western Pacific, has recently been investigated (Meyer and Macurda 1980), but comatulid crinoids in the central Pacific remain largely unknown.

The Marshall Islands occupy a key mid-Pacific position (Figure 1) and represent the

northeastern limit of distribution for Indo-West Pacific comatulids, which are absent from the Hawaiian Archipelago. I have reported (Zmarzly 1984) on the distribution of shallow-water crinoids at Enewetak Atoll, M.I., documenting the occurrence of six species in three families. The reader is also referred to a short review of Enewetak Crinoidea by Devaney (in press).

Records of comatulids from other atolls in the Marshall Islands are largely the result of three systematic collecting efforts, the earliest by the Swedish expedition to the South Sea Islands in 1917, the next during Operation Crossroads in 1946, followed directly by the Bikini Scientific Resurvey in 1947. The crinoids from the Swedish expedition were re-

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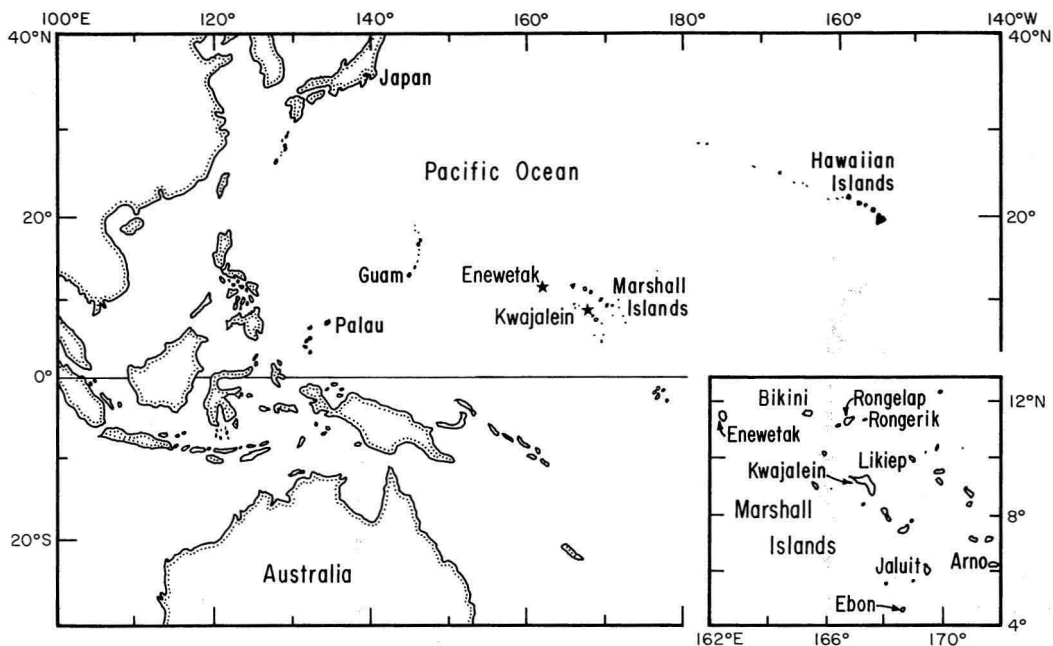


FIGURE 1. Map of the Pacific Ocean, showing the location of the Marshall Islands. Inset shows location of atolls within the Marshall Islands.

ported by Gislén (1940); those from the latter two collections were treated together by Clark (1952). These reports documented a total of seven species from six atolls: Bikini, Ebon, Jaluit, Likiep, Rongelap, and Rongerik (Figure 1). *Comanthus bennetti*, one of the seven species mentioned above, has also been reported from Arno Atoll (Clark 1954) and from Enewetak and Kwajalein atolls as the host of a galatheid crab (Holthuis 1953), as the host of alpheid shrimps (Banner 1959; Banner and Banner 1968), as the host of pseudanthesiid copepods (Humes 1972), and in an echinoderm pigment study (Bartolini et al. 1973).

This paper presents the results of a comprehensive survey of the shallow-water crinoid fauna at Kwajalein Atoll (9°00' N, 167°40' E), 485 km southeast of Enewetak. The survey was conducted as part of a larger study on Indo-West Pacific comatulids and their symbiont faunas. Twelve comatulid species in three families were collected; these are listed in Table 1. The 24-hr exposure patterns of most species are described here, many for the first

time. A field identification key for shallow-water crinoids of the Marshall Islands is provided. Current Marshall Islands crinoid records are summarized, and crinoid faunas are compared between atolls in the Marshalls and between Indo-West Pacific island groups for which comparable data exist.

MATERIALS AND METHODS

Scuba diving surveys of the shallow-water crinoid fauna at Kwajalein were conducted both day and night over a 3-week period in December 1983. The sites investigated encompassed a depth range of 3 to 36 m and are plotted in Figure 2. For logistic reasons, diving effort was concentrated at the southern end of the atoll, mainly on leeward seaward reefs due to the strength of the northeasterly trade winds. When wind and tidal conditions permitted, crinoids were obtained from patch reefs in Gea Pass and from a number of lagoon pinnacles and patch reefs. Reefs at the northern end of the lagoon (near North Pass)

TABLE 1
CRINOIDEA OF KWAJALEIN ATOLL

FAMILY AND SPECIES	CLOSEST PREVIOUS RECORD
COMASTERIDAE	
<i>Comantheria briareus</i> (Bell)	Palau, C. I.
<i>Comanthina schlegeli</i> (P. H. Carpenter)	Enewetak, M. I.
<i>Comanthus bennetti</i> (J. Müller)	Kwajalein, M. I.
<i>Comanthus parvicirrus</i> (J. Müller)	Enewetak, M. I.
<i>Comaster gracilis</i> (Hartlaub)	Bikini, M. I.
<i>Comaster multifidus</i> (J. Müller)	Gilbert Islands
<i>Comatella maculata</i> (P. H. Carpenter)	Truk and Mortlock, C. I.
<i>Comissia</i> sp. cf. <i>C. pectinifera</i> A. H. Clark	Kei Islands (<i>C. pectinifera</i>)
MARIAMETRIDAE	
<i>Lamprömetra palmata</i> (J. Müller)	Likiep, M.I.
<i>Liparometra regalis</i> (P. H. Carpenter)	Tonga
<i>Stephanometra indica</i> (Smith)	Rongelap and Rongerik, M. I.
COLOBOMETRIDAE	
<i>Cenometa bella</i> (Hartlaub)	Jaluit Atoll, M. I.

were surveyed for species present during two dives. Consecutive day and night surveys at a single locality enabled determination of the diel activity patterns of most species.

Crinoids were identified by using both the key of Clark and Rowe (1971) and the systematic descriptions given by Clark (1931, 1941, 1947). D. L. Meyer, University of Cincinnati, kindly provided taxonomic advice. Representative specimens will be deposited with the Division of Invertebrate Zoology, Bernice P. Bishop Museum, Honolulu.

COMASTERIDAE

Comantheria briareus (Bell)

This species has not been reported previously from the Marshall Islands. Clark and Rowe (1971) showed records of *Comantheria briareus* concentrated in the western Pacific. Its range was only recently extended to Palau (Meyer and Macurda 1980), which represents the closest previous record.

Comantheria briareus, the largest comatulid at Kwajalein, characteristically appeared as a dense mass of arms. Individuals were conspicuous on prominent coral or limestone projections both day and night. Since *C. briareus* totally lacks cirri (Figure 3A), animals were tethered to their perch by the lower arms and

pinnules. Attachment by the lower arms created a pedestal which elevated the calyx several centimeters above the substrate (Figure 3B).

This species was observed only on seaward reefs at Kwajalein, at depths exceeding 22 m. In Palau, Meyer and Macurda (1980) found *C. briareus* no deeper than 12 m, but the behavior and bathymetric distribution of another form, which they referred to as *Comantheria* sp. cf. *C. briareus*, was similar to that of specimens referred to here as *C. briareus*.

A very consistent, striking coloration was noted for this species. The division series and brachials were greenish yellow. Some pinnule groups were black with white tips; these groups alternated with groups of pinnules which were proximally white, then black with white tips (Figure 3B).

Comanthina schlegeli (P. H. Carpenter)

Comanthina schlegeli, previously reported from Enewetak Atoll (Bruce and Zmarzly 1983; Zmarzly 1984), has not been recorded elsewhere in the Marshall Islands.

Individuals were fully exposed on coral substrates both day and night. This crinoid was typically found on seaward reef slopes between 6 and 20 m depth, although occurrence was patchy. Juveniles (10 to 12 arms

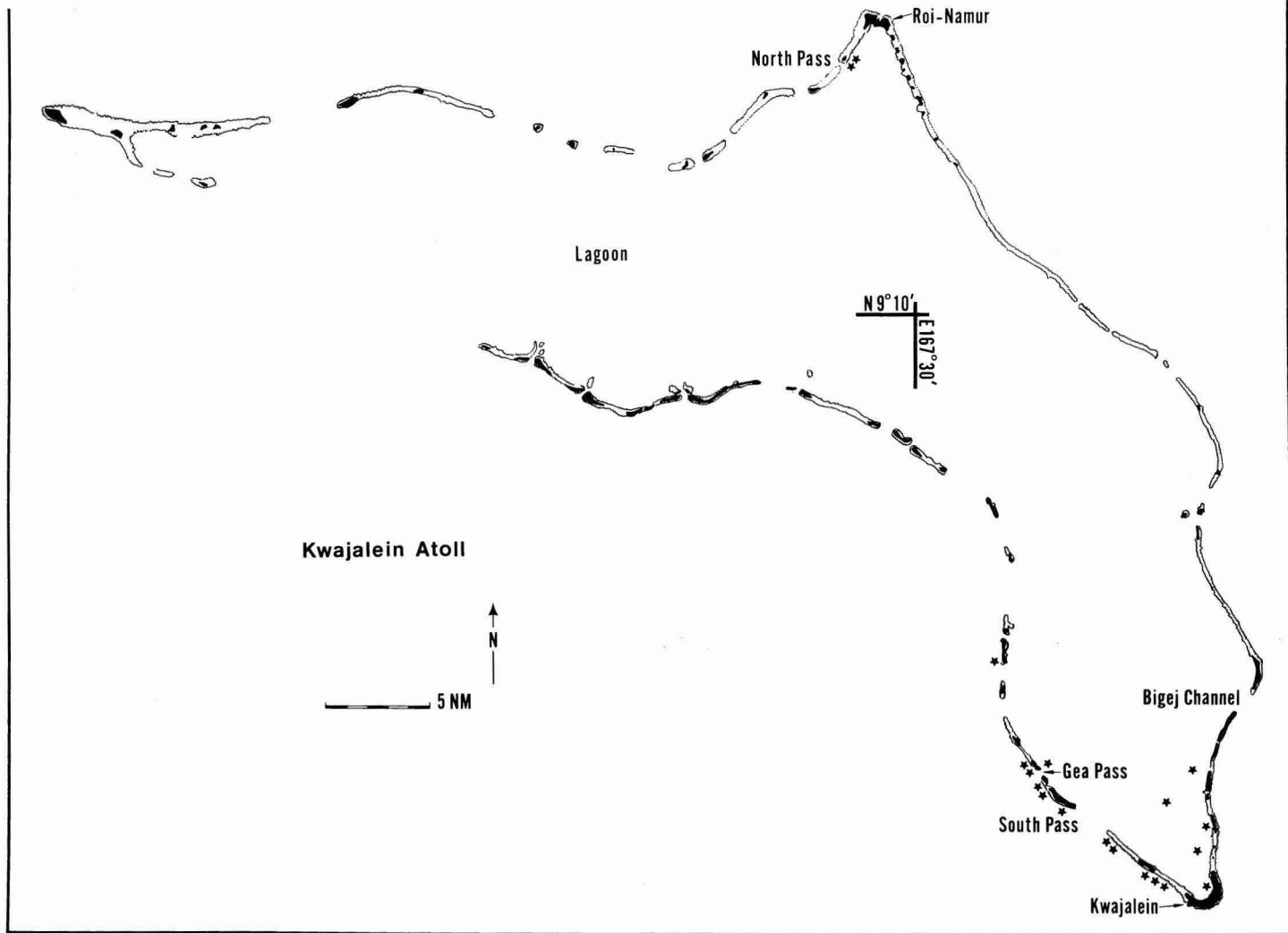


FIGURE 2. Map of Kwajalein Atoll, showing locations of sites surveyed for crinoids in the present study. Note especially the location of sites relative to major tidal passes.

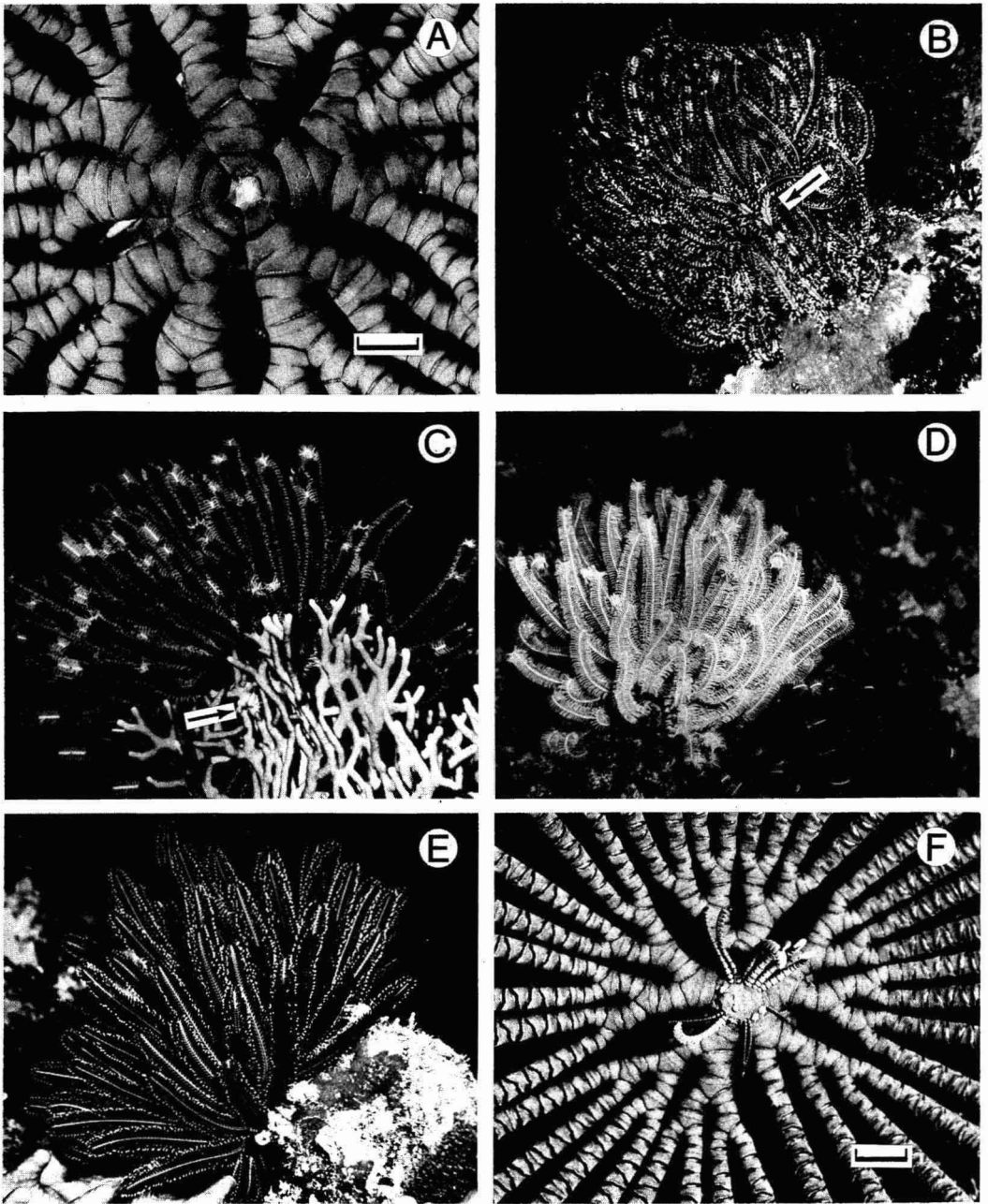


FIGURE 3. *A*, Aboral view of *Comantheria briareus*, showing centrodorsal (2.5 mm in diameter) devoid of cirri. *B*, Posture of *Comantheria briareus* in situ. Note that the lower arms are used to tether the animal to its perch. Arrow indicates level of elevation of calyx above substrate. Arm length (free arm) about 14 cm. *C*, *Comanthina schlegeli* in situ, showing cirri (indicated by arrow) grasping a branch of *Millepora*. Arm length about 15 cm. *D*, *Comanthina schlegeli*, showing two color varieties and typical posture in the absence of current. *E*, Posture assumed by *Comanthus bennetti* during moderate current. Arm length about 18 cm. *F*, Aboral view of *Comanthus parvicirrus*, showing cirri in a single marginal row around the centrodorsal and frequently restricted to the interradial angles. Cirri 8–9 mm in length. Scale \neq 5 mm in *A*, *F*.

approximately 45 mm in length) were also encountered in this habitat, in protected areas under ledges. Occurrence of *C. schlegeli* in the lagoon at Kwajalein was restricted to reefs near the entrances to major passes, such as Gea Pass and North Pass (see Figure 2), with good exposure to daily tidal currents. In and near these passes, individuals were large and common; both size and abundance decreased with distance from the passes. This crinoid most often co-occurred with another rheophilic species, *Comanthus bennetti*.

Morphology and behavior of *C. schlegeli* at Kwajalein were consistent with that observed at Enewetak (Zmarzly 1984). In particular, the cirri were short but well developed (Figure 3C). Although cirri were present, attachment to the substrate was facilitated by several of the lower arms. The rest of the arms were generally held in a dense meridional array which covered the oral disk. During slack water, the arm tips often curled into tendrils (Figure 3D).

The color varieties described for *C. schlegeli* at Enewetak (Zmarzly 1984: table 2) were conserved at Kwajalein, with the addition of one variety which was black with white variegations on the arms and white-tipped pinnules. Thus, as at Enewetak, black or orange-brown arms with white or yellow variegations (encompassing both brachials and pinnules) in bands 1–2 cm in length were characteristic of the species (Figure 3C).

Comanthus bennetti (J. Müller)

Comanthus bennetti was the only comatulid species previously known from Kwajalein, reported first by Holthuis (1953) as the host of a galatheid crab and later by Banner (1959) as the host of an alpheid shrimp. Elsewhere in the Marshall Islands, the species is known from Arno, Enewetak, and Rongelap atolls (Zmarzly 1984).

Widely distributed in the Indo-West Pacific, *C. bennetti* is generally one of the most abundant crinoids where it occurs (Meyer and Macurda 1980; Zmarzly 1984; pers. obs. elsewhere in the tropical Pacific). At Kwajalein, as at Enewetak, this species was a conspicuous and relatively abundant member of the crinoid

fauna in certain habitats. A true rheophile, *C. bennetti* was absent from reefs in the interior of the lagoon but was common in the lagoon on reefs near the entrances to major passes. On seaward reefs where conditions were suitable, individuals were scattered on reef slopes between 6 and 20 m depth, commonly co-occurring with *Comanthina schlegeli*. A juvenile *C. bennetti* (11 arms approximately 70 mm in length) was collected from underneath an adult in this habitat.

Comanthus bennetti occupied coral perches to which it clung with its robust cirri (Figure 3E; see also Zmarzly 1984: figs. 3a and 3b). The behavior of *C. bennetti* did not change in response to day/night cycles, but changes in posture were correlated with current velocity. Postures and behavior typical for the species under various current regimes were described by Meyer and Macurda (1980) and Meyer et al. (1984).

Three of the four recurring color varieties described for *C. bennetti* at Enewetak (Zmarzly 1984: table 3) were also observed at Kwajalein:

CB1: oral disk, division series, and brachials black with an iridescent green speckling; cirri black; pinnules black with either yellow or orange tips

CB2: oral disk yellow, sometimes dusted with black or green; cirri black; division series and brachials yellow; pinnules yellow proximally, then black with either yellow or orange tips

CB4: oral disk and cirri orange-brown; division series and brachials either brown, orange, or orange-brown; pinnules orange to brown with yellow tips or orange tips

CB1 has been observed at locations as widely separated as the Great Barrier Reef, Truk, in the eastern Caroline Islands, the Marshall Islands (Zmarzly 1984; pers. obs.), and Palau, in the western Caroline Islands (Meyer and Macurda 1980). It was the predominant color variety at both Enewetak (Zmarzly 1984) and Kwajalein. CB2 and CB4 were comparatively rare at Kwajalein. Two additional varieties, not observed at Enewetak, were also noted. The first was completely bright yellow. In the

second, the brachials had a median black stripe flanked on either side by a narrow yellow stripe; the pinnules were yellow, but the proximal one-third of each pinnule was dusted with black.

Comanthus parvicirrus (J. Müller)

This species was previously known from the Marshall Islands only at Enewetak Atoll (Zmarzly 1984). At Kwajalein, *C. parvicirrus* was a member of the nocturnal crinoid fauna. It was generally hidden within the reef infrastructure by day, although the arm tips were occasionally visible in crevices or coral heads. The arms of *C. parvicirrus* were more often visible by day at Enewetak than at Kwajalein. This species was observed to emerge fully at night, occupying low or protected coral substrates at sites exposed to current flow and raised substrates at sites without strong currents.

This crinoid was found both in the lagoon and on seaward reefs at Kwajalein. It occurred at sites with strong currents but was also abundant on pinnacles and patch reefs well within the lagoon where current flow was minimal. On the seaward reef, *C. parvicirrus* was common on the reef flat at 6 m depth and was observed to at least 18 m depth.

Comanthus parvicirrus is reported to be an extremely variable species which displays a considerable range in color and morphology (Meyer and Macurda 1980; Clark 1931). Specimens referred to *C. parvicirrus* from both Enewetak and Kwajalein were of a single color variety, solid black. Morphology was consistent between the two locations and conformed well with the description given by Clark (1931).

The cirri were weakly developed, ranging in number from 3 to 12 and from 9 to 10 mm in length. The cirral sockets were arranged in one marginal row around the centrodorsal; occurrence of cirri was frequently confined to the interradial angles (Figure 3F).

The number of arms ranged from 36 to 50; free arm length was 12–14 cm. Most axillaries gave rise to either two division series or two arms, and less frequently to one of each. The IBr series were all composed of two ossicles.

The IIBr series were nearly always of four ossicles, with 3 + 4 united by a syzygy, but occasionally were only of two. The IIIBr were invariably four (3 + 4), as were the IVBr when present. Syzygies on the free arm occurred between brachials 3 + 4, again from between 11 + 12 to between 14 + 15, and distally at intervals of usually five articulations (Figure 4).

Comaster gracilis (Hartlaub)

Although known from Enewetak Atoll (Zmarzly 1984) and Bikini Atoll (Clark 1952), this species has not been reported previously from Kwajalein.

A considerable amount of controversy has surrounded the separation of *Comaster gracilis* and *C. multifidus* (see Clark 1931: pp. 433–434), the only two species in the genus that lack cirri (Clark and Rowe 1971). Hartlaub (1893, cited in Gislén 1940) originally described *gracilis* as distinct from *multifidus* on the basis of its smaller size, its more slender division series, the absence of subradial clefts, and the lack of lateral contact between the IBrl. Clark (1931) later admitted a large amount of morphological variation in both species and relied heavily on size and coloration for their separation. Gislén's (1940) studies demonstrated that coloration is not a reliable feature for distinguishing the two species and that lateral separation of the IBrl is a characteristic of young age rather than one of specific distinction. He concluded that the two species are best distinguished by presence or absence of subradial clefts since "in *multifidus* these clefts appear already at a very juvenile stage."

Both species were tentatively recognized in the Kwajalein material. Upon reexamination, the Enewetak material reported in Zmarzly (1984) was also found to contain representatives of both species. Although separation by standard morphological criteria was difficult, the species were quite distinct in their diel activity patterns, as observed at Kwajalein. From Table 2, which summarizes morphological data for the two species, only two major differences are apparent: the arms of *multifidus* are three times the length of the arms of *gracilis*; and although its arms were shorter,

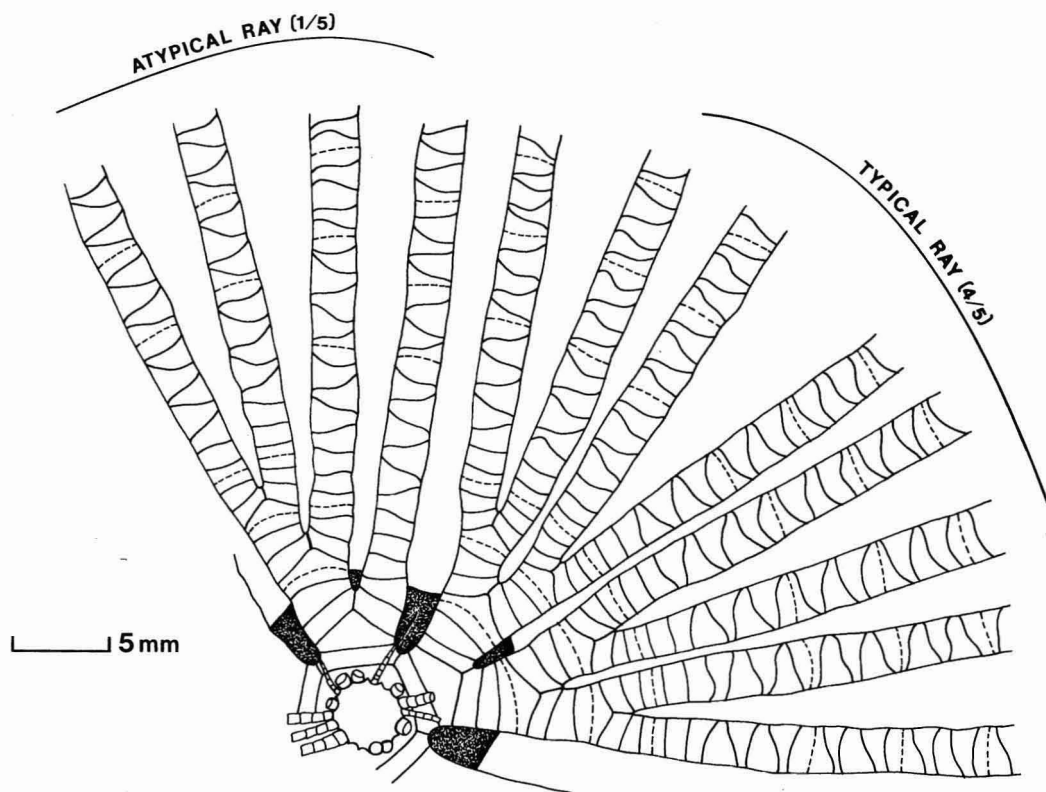


FIGURE 4. Aboral view of *Comanthus parvicirrus*, showing branching pattern and location of syzygies. Note that on the "typical" rays (four of five in the present specimen), axillaries bear two arms or two division series, not one of each; on an "atypical" ray, axillaries may bear one arm and one division series.

TABLE 2

COMPARISON OF TAXONOMICALLY IMPORTANT MORPHOLOGICAL CHARACTERS BETWEEN *Comaster gracilis* AND *C. multifidus* FROM THE MARSHALL ISLANDS

CHARACTER	<i>Comaster gracilis</i> (n = 3)	<i>Comaster multifidus</i> (n = 2)
No. of ossicles in		
IBr	2	2
IIBr	4, rarely 2 (1/30)*	4, occasionally 2 (2/20)
IIIBr	all 2	2, rarely 4 (2/33)
IVBr	2, rarely 4 (1/45)	all 2
VBr	all 2	none present
VIBr	2 when present	none present
First syzygy, free arm	1 + 2	1 + 2, rarely 2 + 3
Second syzygy, free arm	9 + 10 to 12 + 13	8 + 9 to 10 + 11, rarely 4 + 5
No. articulations between subsequent syzygies	3, sometimes 4	3
Length of IBrl in lateral contact	0 to one-half	two-thirds
Color in life	brown	golden orange
No. of arms (mean)	51–76 (61)	41–46 (43.5)
Length of free arm	8–10 cm	up to 31 cm

*Numbers in parentheses represent cumulative observed frequencies of the rare condition in all specimens examined.

gracilis consistently had a greater number of arms than *multifidus*, which eliminates the possibility of its being a juvenile form of the latter. The centrodorsal of each species is stellate, but they differ slightly in configuration (Figure 5; Figure 6A, B). Note that subradial clefts are present in both cases, but the clefts are larger and deeper in *multifidus*. Another difference noted in the present specimens is that the distal ends of the brachials are more finely spinose in *gracilis*; this condition is not well developed in *multifidus*.

Only the smallest specimen of *gracilis* had the IBrl laterally free (Figure 5A); in larger specimens, the IBrl were in contact for up to half of their length (Figure 5B), thus supporting Gislén's contention that laterally free IBrl is a juvenile character. Meyer (pers. comm.) found the state of the IBrl to be useful in distinguishing *gracilis* and *multifidus* in Australia but found that among his Palauan material only the smaller specimens of *gracilis* had the IBrl free.

At Kwajalein, *Comaster gracilis* occurred both in the lagoon and on seaward reefs, at sites with and without exposure to strong current flows. Its distribution was coincident with that of *C. multifidus* and *Comanthus parvicirrus*. Meyer and Macurda (1980) also noted the similarity between *gracilis* and *parvicirrus* in living habits and distribution on Palauan reefs.

Comaster gracilis was generally cryptic by day, hidden within coral thickets or under limestone rubble. Individuals emerged fully at night to occupy low-relief substrates in areas exposed to currents (seaward reef sites; Figure 6C) and prominent perches raised above the substrate in areas where currents were weak (lagoon patch reefs).

All individuals were solid reddish brown to dark brown in coloration.

Comaster multifidus (J. Müller)

Although known from several localities in the Gilbert Islands (Gislén 1940), *Comaster multifidus* has not previously been reported from Kwajalein or the Marshall Islands. This species has now also been recognized in collections from Enewetak.

During the day, this crinoid extended its long, delicate arms from crevices in the reef, while keeping its oral disk and the basal portions of its arms hidden (Figure 6D). As cirri are totally lacking (Figure 6B), the pinnules on the basal portions of the arms were used to hold the animal in place. Nocturnal observations revealed that the arms often remained extended through the night, but, unlike *C. gracilis*, there was no further emergence.

All specimens were golden orange to orange-brown in coloration. The common golden orange variety of *C. gracilis* reported by Zmarzly (1984: fig. 3D) at Enewetak is now recognized as *C. multifidus*.

Comatella maculata (P. H. Carpenter)

This species is known from the western Indian Ocean and several localities throughout the Pacific, but it has never been reported from the Marshall Islands. The closest previous records were Truk and the Mortlocks in the eastern Caroline Islands (Clark 1931).

Comatella maculata was completely cryptic by day but emerged fully at night to occupy coral perches. Comparatively rare among the nocturnal species, it was observed only at one seaward reef site between 6 and 16 m depth. The few specimens encountered were solid dark purple in color; the pinnules had golden orange tips. This crinoid is small in size and has 20 arms approximately 75 mm in length. The present specimen agrees closely with the description given by Clark (1931).

Comissia sp. cf. *C. pectinifera* A. H. Clark

Literature records of *Comissia pectinifera* are rare. The species is known from only three localities: Christmas Island, between Sumatra and Java; the Kei Islands, near New Guinea (Clark 1931); and the Maldive Islands (Clark and Davies 1965).

The range of variation within the species is currently defined by five specimens, complicated by the fact that *C. pectinifera* closely resembles *C. lütkeni*. Morphological characters of taxonomic importance are summarized in Table 3 for *lütkeni*, *pectinifera*, and two specimens (one small and one large) collected

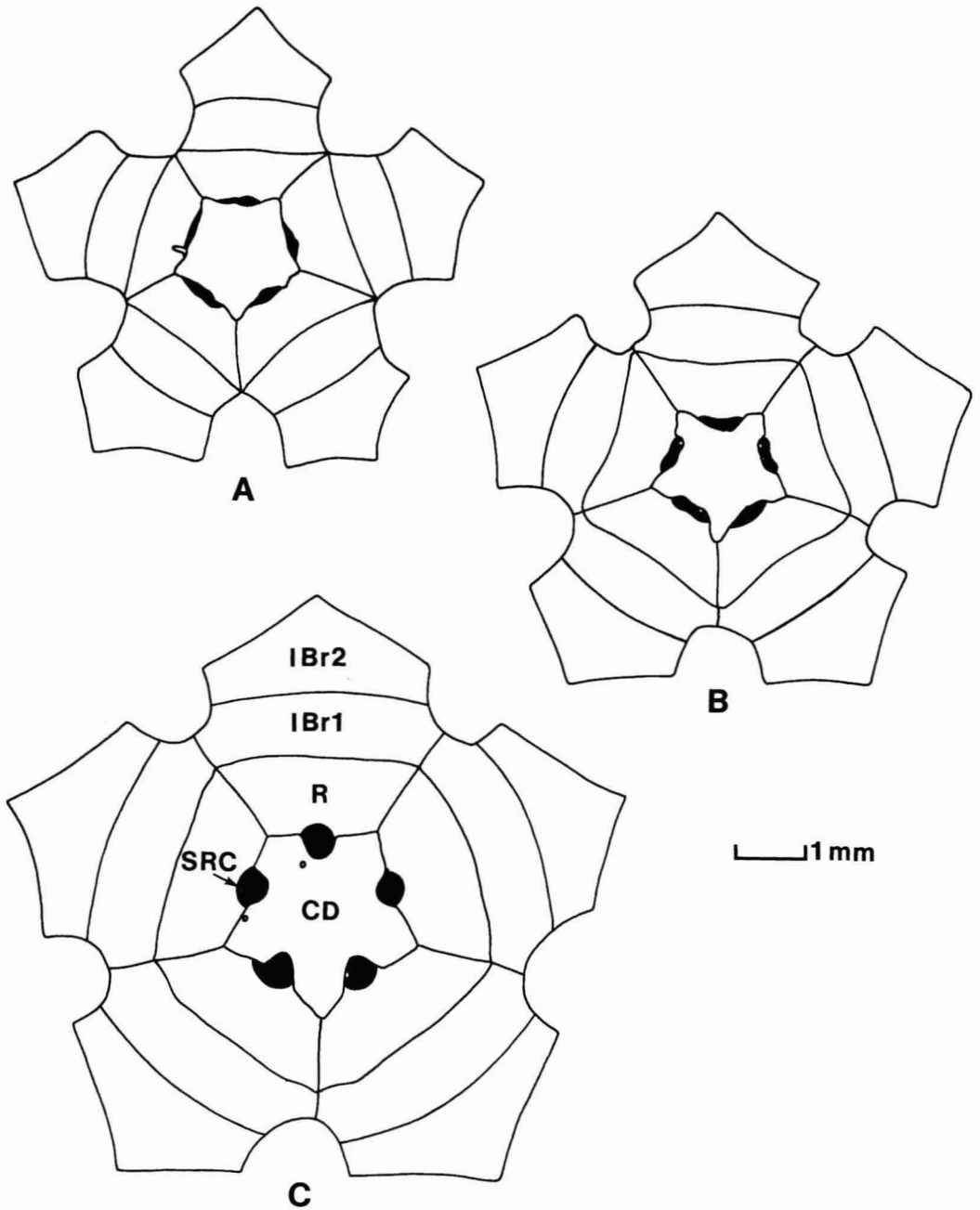


FIGURE 5. Aboral view of centrodorsal (CD), radials (R), subradial clefts (SRC), and IBr series: A, *Comaster gracilis*, 51 arms; B, *C. gracilis*, 56 arms; C, *C. multifidus*, 41 arms.

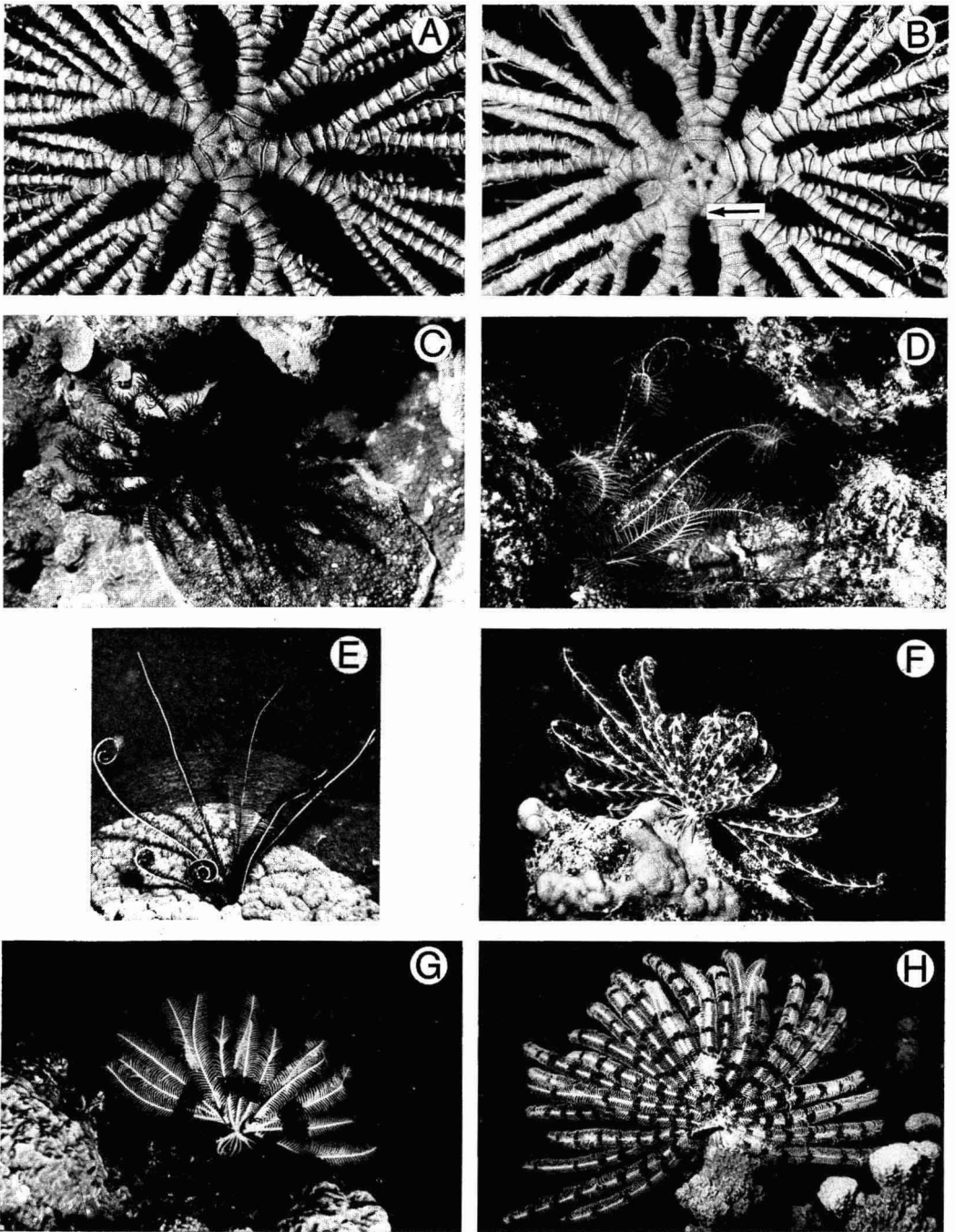


FIGURE 6. *A*, Aboral view of *Comaster gracilis*; note stellate centrodorsal (1.5 mm in diameter) and narrow subradial clefts as compared with Figure 6*B*. Some of the IBrl are in partial contact. *B*, Aboral view of *Comaster multifidus*, showing stellate centrodorsal (2.5 mm in diameter) and deep subradial clefts; note that the IBrl are in lateral contact for at least half of their length. *C*, *Comaster gracilis*, showing its full emergence from the reef at night. Arm length about 8–10 cm. *D*, Typical degree of exposure of *Comaster multifidus*, both day and night. Arm length up to 31 cm. *E*, Nocturnal emergence of arms of *Comissia* sp. cf. *C. pectinifera* from the coral *Lobophyllia*. The ten arms were approximately 35 cm in length. *F*, *Liparometra regalis* after nocturnal emergence, showing characteristic color pattern. Arm length about 14 cm. *G*, *Stephanometra indica* at night, at 6 m depth on the seaward reef. Arm length about 8 cm. *H*, *Stephanometra indica* photographed at 2015 hours, showing variegated color pattern. Arm length reached 10–11 cm.

TABLE 3

COMPARISON OF MORPHOMETRIC AND MERISTIC DATA BETWEEN *Comissia lütkeni*, *C. pectinifera*, AND SPECIMENS IN THE PRESENT COLLECTION REFERRED TO AS *Comissia* sp. cf. *C. pectinifera*

CHARACTER	<i>Comissia lütkeni</i>	<i>Comissia pectinifera</i> A. H. CLARK		KWAJALEIN SPECIMENS	
	A. H. Clark	HOLOTYPE*	MALDIVES SPM.†	LARGE	SMALL
Cirri					
No. of cirri	15–25	14 34 (23, 33)	“c. 45”	33	11
No. segments/cirrus	16–24 (usually 18–21)	14–16 (usually 16)	15–19	16–18	14–16
Length of cirri	7–17 mm	14 mm (15–17 mm)	NR	14–15 mm	11–12 mm
Transition segment	4th (occasionally 5th)	8th (6th)	6th, 8th–10th	6th or 7th	6th or 7th
Arrangement of cirri	2 alternating rows	3 alternating rows	“2 or 3 crowded rows”	3 alternating rows	
Pinnule combs					
No. of pinnules with combs	P1–P4	P1–P4	P1–P4, P1–P5 on one arm	P1–P4	P1–P4
No. of comb teeth, P1	16	25 (29–33)	NR	26–59	30
No. of comb teeth, P4	NR	15–16 (25–26)	15	30	23–25
Arms					
Length of free arm	70–75 mm, up to 100 mm	90 mm (100, 110 mm)	arms broken at 60 mm; estimated to reach “c. 90 mm”	350 mm	140–150 mm
First syzygy, free arm	3 + 4	3 + 4	3 + 4	3 + 4	3 + 4
Second and distal syzygies	from 11 + 12 to 14 + 15, distally at intervals of 3 muscular articulations	same as <i>C. lütkeni</i>	NR	from 11 + 12 to 13 + 14, distally at intervals of usually 3 muscular articula- tions (occasionally 4–6)	
No. of specimens	13	1 (3)	1	1	1
Geographic range	Lesser Sunda Is. to Queensland and Philippine Is.	Christmas Is., Kei Is., to Maldives		—	—

NOTE: Data for *C. lütkeni* and the holotype and Kei Islands specimens of *C. pectinifera* from Clark (1931); Maldives specimen discussed by Clark and Davies (1965). NR = no record.

*Data based on holotype from Christmas Island; numbers in parentheses indicate variation of Kei Islands specimens from holotype.

†Cambridge Museum no. E.278 (pt.).

at Kwajalein. The present specimens are in the main consistent with *C. pectinifera*, except that in the larger specimen the number of comb teeth on both P1 and P4 is rather high and the arm length is more than three times that reported for *C. pectinifera* by Clark (1931). However, my measurements were made on a live, hand-collected specimen with the arms fully intact to the tips. Clark and Davies (1965) stated that the arms of the Maldives specimen were broken and estimated their length to be 90 mm. Data concerning the variability of *C. pectinifera* are inadequate at present to permit a reliable determination of the Kwajalein material.

Comissia sp. cf. *C. pectinifera* was part of the nocturnal crinoid fauna at Kwajalein. It generally occupied living corals, particularly large heads of *Lobophyllia*. By night, only the extremely long arms were extended from crevices in the coral (Figure 6E). This crinoid was entirely cryptic by day and was found to be highly photosensitive; the arms were rapidly coiled and retracted when exposed to a diver's light at night. Small individuals were sometimes completely exposed at night, clinging to coral substrates with their numerous cirri.

Comissia sp. cf. *C. pectinifera* occurred both in the lagoon and on seaward reefs. It frequently co-occurred with *Comaster gracilis*, *C. multifidus*, *Comanthus parvicirrus*, and *Stephanometra indica*.

Two distinct color varieties were noted for this species. In one, the entire animal was solid orange-brown. In the other, the entire animal was dark brown, but the ribs of the arms were light green.

MARIAMETRIDAE

Lamprometra palmata (J. Müller)

Lamprometra palmata was known from three other atolls in the Marshall Islands (Zmarzly 1984) prior to its collection at Kwajalein. The present record is based on a single juvenile specimen, which conforms with the description given by Clark (1941). In particular, P2 is markedly stouter than either P1 or

P3. The specimen was found under coral rubble on the seaward reef flat during the day, at approximately 6 m depth. It was dark purple to brown in color; the cirri were cream, with purple articulations. This species was found to be abundant among the nocturnal crinoids in Palau (Meyer and Macurda 1980).

Liparometra regalis (P. H. Carpenter)

Liparometra regalis was collected by the Challenger expedition in the Tonga Islands in 1874 (Clark 1941) and has not been reported since.

The present specimen has 40 arms which are approximately 14 cm in length. There are about 30 cirri, with 23–29 segments; the cirri reach to one-fifth of the arm length. The distal cirrus segments possess a dorsal ridge or keel. P2 is nearly twice as long as P1, but it is not stout and pronounced as in *Lamprometra palmata*. P2 is generally similar in length to P3 but exceeds P3 in length on some rays.

At Kwajalein, *L. regalis* was strictly nocturnal, being hidden within the reef infrastructure by day. At night, it emerged fully to occupy prominent coral perches at depths of 9–10 m (Figure 6F). Single individuals were observed both on lagoon patch reefs and on seaward reefs, but the species was not common at the sites investigated.

Liparometra regalis had a striking coloration which consisted either of inverted V-shaped bands of reddish brown on white arms or white bands on brown arms (Figure 6F). The numerous, long cirri were white to tan in color.

Stephanometra indica (Smith)

Stephanometra indica was previously known from five different atolls in the Marshall Islands (Zmarzly 1984). This is the first report of the species at Kwajalein.

Stephanometra indica was completely absent from reefs during the day but could easily be found under piles of coral rubble. It emerged fully at night to become the most common and abundant member of the nocturnal crinoid fauna. This species dominated the reef flat at approximately 6 m depth and

was observed to at least 18 m depth. It was found at all the sites surveyed. After emergence, several individuals often occurred in close proximity, but each occupied its own limestone promontory.

Stephanometra indica is extremely light-sensitive and quickly coiled its arms over the oral disk when exposed to the beam of a diving light. It was also capable of active swimming when physically provoked.

The color patterns of this crinoid were extremely variable:

1. Cirri, division series, brachials pinkish purple (the tissue covering the ossicles was generally cream to pink, with purple articulations, giving an overall impression of pinkish purple); pinnules orange.

2. Solid maroon-purple; cirri sometimes white or mottled maroon and white.

3. Cirri proximally white, distally brownish; arms and pinnules completely white but proximal half of each arm with one to three maroon bands (Figure 6G).

4. Cirri, division series, and proximal one-third of arms white (articulations purple); distal two-thirds of each arm maroon.

5. Maroon and white variegated; individuals ranged from predominantly maroon with white variegations to predominantly white with maroon variegations; contrasting bands encompassed the brachials, the pinnules, or both; differences in the length, width, and number of these bands were responsible for the large degree of variation between individuals (Figure 6H). Some individuals had yellow-tipped pinnules.

COLOBOMETRIDAE

Cenometra bella (Hartlaub)

Cenometra bella (as *C. bella* var. *magnifica*) was reported from Jaluit Atoll by Gislén (1940) but has not previously been reported from Kwajalein.

This crinoid was observed at several localities at Kwajalein, but its occurrence appeared to be restricted by both substrate and current requirements. All occurrences of *C. bella*

(as well as its usual substrate, antipatharian corals) were at depths in excess of 25 m, except for an unusual occurrence at 15 m in which case the substrate was a pocilloporid coral. *Cenometra bella* was also occasionally observed clinging to gorgonians. This rheophilic species was found on seaward reefs and only in the lagoon on reefs near the entrances to passes.

The usual mode of occurrence was as single individuals. When two or three individuals occupied the same wire coral, the extended arms occasionally overlapped to form a common filtration fan. Further details of the life habits of this species at Kwajalein were as summarized by Meyer and Macurda (1980) for Palauan specimens.

Two of the commonly reported color varieties were observed at Kwajalein (see Meyer and Macurda 1980: fig. 5f; Faulkner 1974: figs. 26 and 51). Some individuals were all black, while in others the black pinnules were dusted with white to varying degrees and thus appeared silver or gray.

DISCUSSION

Access to Kwajalein has traditionally been restricted because of its use as a missile range by the U.S. Army; hence faunal records for the atoll are rare. Much of the available information is due to the interest that civilian and military personnel stationed on the atoll have taken in marine organisms, particularly mollusks. To date, only a single crinoid species, *Comanthus bennetti*, has been reported from Kwajalein (Holthuis 1953; Banner 1959). The present study documents the occurrence of 11 additional shallow-water species in three families.

The presence of crinoids on reefs at Kwajalein appears to be related to current requirements. In general, the species which were cryptic or semicryptic by day (but emerged to different degrees at night) occurred on seaward reefs but were also the only colonizers of patch reefs and pinnacles in the interior of the lagoon where currents were weak or variable. Members of a second group, comprised predominantly of large, fully exposed comaste-

FIELD IDENTIFICATION KEY FOR SHALLOW-WATER CRINOIDS IN THE MARSHALL ISLANDS*

1.	Anus approximately central, mouth peripheral; terminal segments of proximal pinnules bearing a comb (COMASTERIDAE)	2
1'.	Mouth central, anus peripheral; terminal segments of proximal pinnules without combs, merely tapering to a point (OTHER FAMILIES)	9
2.	Fully or partly visible by day	3
2'.	Cryptic by day, curled up within or beneath living coral; nocturnally active	6
3.	Fully visible by day, generally perched on living coral or limestone promontories in locations exposed to current flow; more than 50 arms	4
3'.	Arms only visible by day emerging from reef; common at most sites regardless of current strength; usually less than 50 arms (Figure 6B, D)	<i>Comaster multifidus</i>
4.	Cirri present	5
4'.	Cirri absent; clings with arms to coral perches; commonly more than 80, up to 150, arms (Figure 3A, B)	<i>Comantheria briareus</i>
5.	More than 20 long cirri, 40–45 mm in length, evenly distributed around centrodorsal; up to 150 but typically 100 or less; conspicuous at locations with good exposure to currents (Figure 3E)	<i>Comanthus bennetti</i>
5'.	Fewer than 20 short cirri, 15–20 mm in length, often discontinuously distributed around centrodorsal; up to 150 arms, typically more than 100 (Figure 3C, D)	<i>Comanthina schlegeli</i>
6.	Fully emerge at night	7
6'.	Arms only emerge at night; 10 arms, widely separated laterally, about 340 mm long (Figure 6E)	<i>Comissia</i> sp. cf. <i>C. pectinifera</i> [†]
7.	No more than 20 arms; cirri well developed, the distal segments with dorsal spines	<i>Comatella maculata</i>
7'.	More than 20 arms	8
8.	Cirri absent; more than 50 arms (Figure 6A, C)	<i>Comaster gracilis</i>
8'.	Cirri present but often rudimentary or confined to interradial angles; 50 arms or less (Figure 3F)	<i>Comanthus parvicirrus</i> [‡]
9.	5 arms only	<i>Eudiocrinus tenuissimus</i>
9'.	More than 5 arms	10
10.	10 arms only	<i>Dorometra nana</i>
10'.	More than 10 arms	11
11.	Fully visible by day; clings to octocorals	<i>Cenometra bella</i>
11'.	Cryptic by day, curled up beneath coral rubble or within coral heads; emerge fully at night	12
12.	P2 stout, larger than P1 and P3	13
12'.	P2 slender, nearly twice as long as P1 but similar in length to P3; cirri stout, about one-fifth of the arm length (Figure 6F)	<i>Liparometra regalis</i>
13.	P2 stiffened and spikelike, form palisade over oral disk; color variable, often maroon and white variegated pattern (Figure 6G, H)	<i>Stephanometra indica</i>
13'.	P2 stiffened only basally; color not as above	<i>Lamprometra palmata</i>

* A diagram and an explanation of morphological terms can be found in Clark and Rowe (1971: p. 3).

[†] Small individuals (arm lengths less than 150–200 mm) were fully exposed on coral substrates at night.

[‡] The arms of *Comanthus parvicirrus* were sometimes visible during the day at Enewetak Atoll but were not frequently observed during the day at Kwajalein.

rids, were restricted in occurrence to seaward reefs and were found on lagoon reefs only in close proximity to tidal passes. These rheophilic species showed a variety of morphological and behavioral adaptations which presumably enable them to inhabit environments where strong currents prevail. Species in the first group appear not to require strong current flow, but their cryptic habits may enable them to invade habitats exposed to currents, as well as more shallow, turbulent areas like the seaward reef flat, from which the exposed comasterids were excluded.

Seven of the twelve species at Kwajalein

were nocturnal; only five species were consistently visible on daytime dives (Table 4). Although not quantified, the density of nocturnal populations clearly exceeded that of day-active populations. Fishelson (1974) noted this pattern in the northern Red Sea, where an estimated 12,000 crinoids (in three species) were visible one night on a 200-m-long coral table. Seventy percent of the individuals belonged to a single species, *Lamprometra klunzingeri*. At Kwajalein, *Stephanometra indica* similarly dominated the nocturnal fauna.

Meyer and Macurda (1980) found 8 of the

TABLE 4

CLASSIFICATION OF SHALLOW-WATER CRINOIDS OF THE MARSHALL ISLANDS ACCORDING TO DIEL ACTIVITY PATTERN

-
- I. Species visible on 24-hour basis
- A. Species fully exposed to view
1. Occupy prominent coral or limestone perches
 - a. *Comantheria briareus*—below 22 m
 - b. *Comanthus bennetti*—3–36+ m
 2. Cling to octocorals
 - a. *Cenometra bella*—as shallow as 15 m but usually deeper than 25 m
 3. Perch on coral but generally in more protected positions
 - a. *Comanthina schlegeli*—3–36+ m
- B. Species semicryptic, dwelling within reef infrastructure or coral formations with only the arms exposed
- a. *Comaster multifidus*—6–36+ m
- C. Species semicryptic, dwelling within caves
- a. *Eudiocrinus tenuissimus*—nocturnal behavior unknown
- II. Species cryptic by day under coral rubble or within coral formations
- A. Species which emerge fully at night onto coral substrates
- a. *Comanthus parvicirrus**
 - b. *Comaster gracilis*
 - c. *Comatella maculata*
 - d. *Lamprometra palmata*
 - e. *Liparometra regalis*
 - f. *Stephanometra indica*
- B. Species which extend only the arms at night, hiding the body within living coral
- a. *Comissia* sp. cf. *C. pectinifera*
- C. Nocturnal behavior unknown
- a. *Dorometra nana*
-

*The arms of *Comanthus parvicirrus* were sometimes visible during the day at Enewetak but were not often seen on daytime dives at Kwajalein.

21 species in Palau to be nocturnal, including *Stephanometra indica*, *Comatella maculata*, and *Lamprometra palmata* as reported here. They found that *Comaster gracilis* and *Comanthus parvicirrus* dwelled within the reef infrastructure but extended their arms by day. These species behaved similarly at Enewetak (Zmarzly 1984), but they were generally more cryptic by day at Kwajalein, emerging fully from coral formations only at night.

Table 5 summarizes published records of crinoids for the Marshall Islands by atoll. At present, the disparity between atolls in the number of species known most likely reflects differences in sampling effort and methods rather than true faunal differences. A tentative comparison, however, can be made between Enewetak and Kwajalein. Although night surveys were conducted at Kwajalein but not at Enewetak, coral rubble was overturned and coral formations were broken open in an effort to reveal species which were cryptic by day at Enewetak. In spite of this, just over half of the species found at Kwajalein were found

at Enewetak. Several factors may account for the observed differences in crinoid faunas between the two atolls. The five species held in common (Table 5) are all wide-ranging comasterids, four of which have an Indo-West Pacific range and one of which is known from the tropical Pacific. The two species found at Enewetak but not at Kwajalein, *Dorometra nana* and *Eudiocrinus tenuissimus*, are small and cryptic forms which could easily have been missed. Of the seven species which occurred at Kwajalein but not at Enewetak, five were nocturnal. The remaining two species, *Comantheria briareus* and *Cenometra bella*, were absent from habitats at Enewetak comparable to those in which they occurred at Kwajalein. These species may have true disjunct distributions.

Disjunct, discontinuous, and patchy distributions have frequently been reported for Indo-West Pacific invertebrates (Kay 1980). Occurrence at some atolls but not others within an island group has been demonstrated for marine gastropods (Kay 1971, 1979; Kay

TABLE 5
RECORDS OF COMATULID CRINOIDS IN THE MARSHALL ISLANDS, UPDATED FROM ZMARZLY (1984)

CRINOID SPECIES	ATOLLS AND COORDINATES WHERE COLLECTED								
	ENEWETAK 11°30' N 162°10' E	BIKINI 11°40' N 165°25' E	RONGELAP 11°10' N 166°30' E	RONGERIK 11°15' N 167°40' E	LIKIEP 10°00' N 169°10' E	KWAJALEIN 9°00' N 167°40' E	ARNO 7°05' N 171°45' E	JALUIT 6°00' N 169°30' E	EBON 4°35' N 168°45' E
COMASTERIDAE									
<i>Comantheria briareus</i> (Bell)	—	—	—	—	—	+	—	—	—
<i>Comanthina schlegeli</i> (P. H. Carpenter)	+	—	—	—	—	+	—	—	—
<i>Comanthus bennetti</i> (J. Müller)	+	—	+	—	—	+	+	—	—
<i>Comanthus parvicirrus</i> (J. Müller)	+	—	—	—	—	+	—	—	—
<i>Comaster gracilis</i> (Hartlaub)	+	+	—	—	—	+	—	—	—
<i>Comaster multifidus</i> (J. Müller)	+	—	—	—	—	+	—	—	—
<i>Comatella maculata</i> (P. H. Carpenter)	—	—	—	—	—	+	—	—	—
<i>Comissia</i> sp. cf. <i>C. pectinifera</i> A. H. Clark	—	—	—	—	—	+	—	—	—
MARIAMETRIDAE									
<i>Lamprometra palmata</i> (J. Müller)	—	—	—	—	+	+	—	+	+
<i>Liparometra regalis</i> (P. H. Carpenter)	—	—	—	—	—	+	—	—	—
<i>Stephanometra indica</i> (Smith)	—	+	+	+	—	+	—	+	+
EUDIOCRINIDAE									
<i>Eudiocrinus tenuissimus</i> Gislén	+	—	—	—	—	—	—	+	—
COLOBOMETRIDAE									
<i>Cenometra bella</i> (Hartlaub)	—	—	—	—	—	+	—	+	—
ANTEDONIDAE									
<i>Dorometra nana</i> (Hartlaub)	+	—	—	—	—	—	—	+	+
TOTAL NO. SPECIES	7	2	2	1	1	12	1	5	3

and Switzer 1974). For comatulids, distributions are known to be patchy within localities, related especially to substrate and current requirements (Meyer and Macurda 1980; Zmarzly 1984). In addition, the extreme northwestern position of Enewetak relative to other atolls in the Marshall Islands removes it from the path of the north equatorial counter-current. This isolation may contribute to true faunal differences between Enewetak and Kwajalein.

Of the 11 new species records for Kwajalein, 5 are new for the Marshall Islands. The addition of these 5 species to the 9 previously reported to occur (Zmarzly 1984) increases the number of shallow-water crinoid species known for the Marshall Islands to 14. Ten of the species have an Indo-West Pacific range, and 4 are known only from the tropical Pacific.

While the majority of species are widely distributed, *Liparometra regalis* is one exception, the only previous record being from Tonga. Both reports of *Eudiocrinus tenuissimus* are currently from the Marshall Islands (Gislén 1940; Zmarzly 1984), but this species is likely to be synonymous with *E. eoa*, which was described by Clark (1941) based on a specimen from the Philippines. I examined the holotype specimen of *E. eoa*, deposited at the U.S. National Museum, but it was so badly disintegrated that no characters of taxonomic value were discernible. Although Clark's description of the species is incomplete, he described the cirri in detail and concluded that "the . . . cirri . . . distinguish this species from all the others in the genus." The cirri of *E. eoa*, however, conform exactly to those of *E. tenuissimus* as described by Gislén (1940). Clark's (1941) treatment of the genus *Eudiocrinus* does not include *tenuissimus*, which was described just a year before and which appears to have been unknown to him. The lack of further records of *E. tenuissimus* is probably due to its small size and cryptic behavior.

The crinoid fauna at this mid-Pacific location was dominated by members of the family Comasteridae (8 of 14 species). The Mariametridae were represented by three species, and the Colobometridae, Antedonidae, and Eudiocrinidae were each represented by a sin-

gle species. Himerometrid comatulids, which are common in the western Pacific, were absent from the Marshall Islands as they were from Palau (Meyer and Macurda 1980).

Given the current state of crinoid taxonomy, especially the inadequacy of data concerning intraspecific variation, and the lack of comparable studies within island groups, a detailed analysis of zoogeographic patterns would be premature. However, it is possible to compare the diversity and taxonomic composition of crinoid faunas between the Marshall Islands and Palau, where surveys of comparable duration, intensity, and scope have been conducted. Fourteen species occur in the Marshall Islands, compared to 21 for the Palau Archipelago. Eleven of the species are shared. The remainder of the species found in Palau, but absent from the Marshall Islands, were mariametrids and colobometrids with western Pacific affinities. Thus, the Marshall Islands comatulid fauna is predominantly an attenuated western Pacific fauna. It is doubtful that *Eudiocrinus tenuissimus* is endemic, but this question awaits further study.

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