Ecology and Distribution of the Shallow-Water Crinoids of Palau and Guam[1]

DAVID L. MEYER

Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221

D. BRADFORD MACURDA, JR.

Exxon Production Research Corporation, P. O. Box 2189, Houston, Texas 77001

Abstract.—Scuba diving investigations in the Palau Islands and Guam, plus previous records, have revealed a total of 21 species of comatulid (unstalked) crinoids in Palau and 7 species in Guam occurring at depths to 40–50 m. An additional comatulid species is recorded from 180–300 m in Palau and a stalked crinoid is recorded from 360 m in Guam. All are new records except for six species previously known from Palau. Of the 17 shallow-water species for which feeding habits are known, 11 species form filtration feeding fans, while 6 species are totally or partially nocturnal. The distribution of crinoids in the Palauan archipelago shows the highest concentrations of species and individuals to be located within the fringing barrier reef, particularly in tidal passes and at other sites where currents prevail. A key based on color in life and living habits is presented for the shallow-water crinoids of Palau and Guam.

Introduction

This study represents the first attempt to make a comprehensive survey of the composition and ecology of a diverse comatulid (unstalked) crinoid fauna inhabiting shallow waters (to 40 m) in the western Pacific. The richness of the shallow-water crinoid fauna of the Indo-West Pacific (138 spp. listed by Clark and Rowe, 1971) contrasts sharply with that present at similar depths in the tropical western Atlantic (8 spp., Meyer, 1973a; Meyer et al., 1978).H. L. Clark (1915) pioneered field studies of comatulid crinoids with his study of 22 species at Torres Strait, northern Great Barrier Reef. Although some of the species Clark listed have since been synonymized, the high diversity he reported is consistent with our own findings at Lizard Island, farther to the south (Meyer and Macurda, 1977) and those of R. A. Birtles (pers. comm.). In situ observation of the feeding behavior and ecology of comatulid crinoids was initiated by Magnus (1963), who studied a single species in the Red Sea. Further work in the Red Sea has been reported by Rutman and Fishelson (1969) and by Fishelson (1974). Fishelson discussed the ecology of 14 species occurring from the shallow subtidal to depths of 45–50 m. The record of 20 species reported here from Palauan shallow waters is exceeded only by the diversity of Great Barrier Reef faunas and probably by faunas from Indonesia (Meyer, 1976, and unpublished).

[1] Contribution No. 125, University of Guam Marine Laboratory.

Micronesica 16(1): 59–99. 1980 (June).

Methods

Our investigation of the shallow-water crinoids in the Palau Islands (Fig. 1) was carried out during two visits totaling nine weeks' duration during 1976 and 1977. For logistical reasons, the study was restricted to the southern half of the archipelago, from the Koror-Babeldaob channel to the north to Bailechesengel in the south (Fig. 2). Our approach was to survey as many habitats as possible diving with scuba and snorkeling in order to determine species composition and distribution of crinoids from the intertidal to depths of about 40 m. A total of 96 dives was made, each involving the efforts of up to 3 divers in locating and observing crinoids. Table 1 lists the crinoids recorded from these surveys in Palau; Table 2 lists crinoid species recorded from four dives in Guam as well as a stalked crinoid from greater depth. Previous records are included. Table 3 lists the principal diving sites, plotted in Figure 2, the number of dives per site, and the crinoid species found at each site.

Underwater photographs were taken to record the living positions, preferred substrata, and color variations of crinoids observed. Specimens were collected by placing them in closable plastic containers, and were preserved by immersion in a shallow pan of 95 percent ethanol followed by fixation in 70 percent ethanol. Commensal organisms were separated during preservation. We found the key presented by Clark and Rowe (1971) very useful for making first order identifications of Palauan crinoids. These identifications have been followed up by comparison to the extensive descriptions provided by A. H. Clark's MONOGRAPH OF THE EXISTING CRINOIDS (1915–50; Clark and Clark, 1967). Additional field data were collected on current conditions, feeding behavior, and relative abundance. A quantitative survey of distribution and abundance of nocturnal crinoids at one site was conducted which will be reported on in a separate publication. Laboratory studies of the stomach and fecal contents of several crinoid species are also in progress.

TERMINOLOGY

Five general feeding postures have been observed among the Palauan species: 1) arcuate fan, 2) radial fan, 3) parabolic fan, 4) arm fan, and 5) multidirectional posture. Within each of these general feeding postures, variations peculiar to individual species are apparent. The five general feeding types are defined as follows:

1) ARCUATE FAN: The crinoid perches on an exposed pinnacle of the reef framework and extends the arms perpendicular to the prevailing current (Fig. 3a). The shape of the arm array can vary depending on the configuration of the substratum from an arc greater than 90 degrees to an arc greater than 180 degrees. The arcuate fan will generally possess two layers of arms because it is formed by the folding in half of a circular array of arms radiating from the central disk. Those arms in the layer on the downcurrent side of the fan frequently twist so that the ambulacral grooves face downcurrent. The arcuate fan has been previously referred to as the vertical filtration fan (Magnus, 1963; Breimer, 1969; Meyer, 1973a).

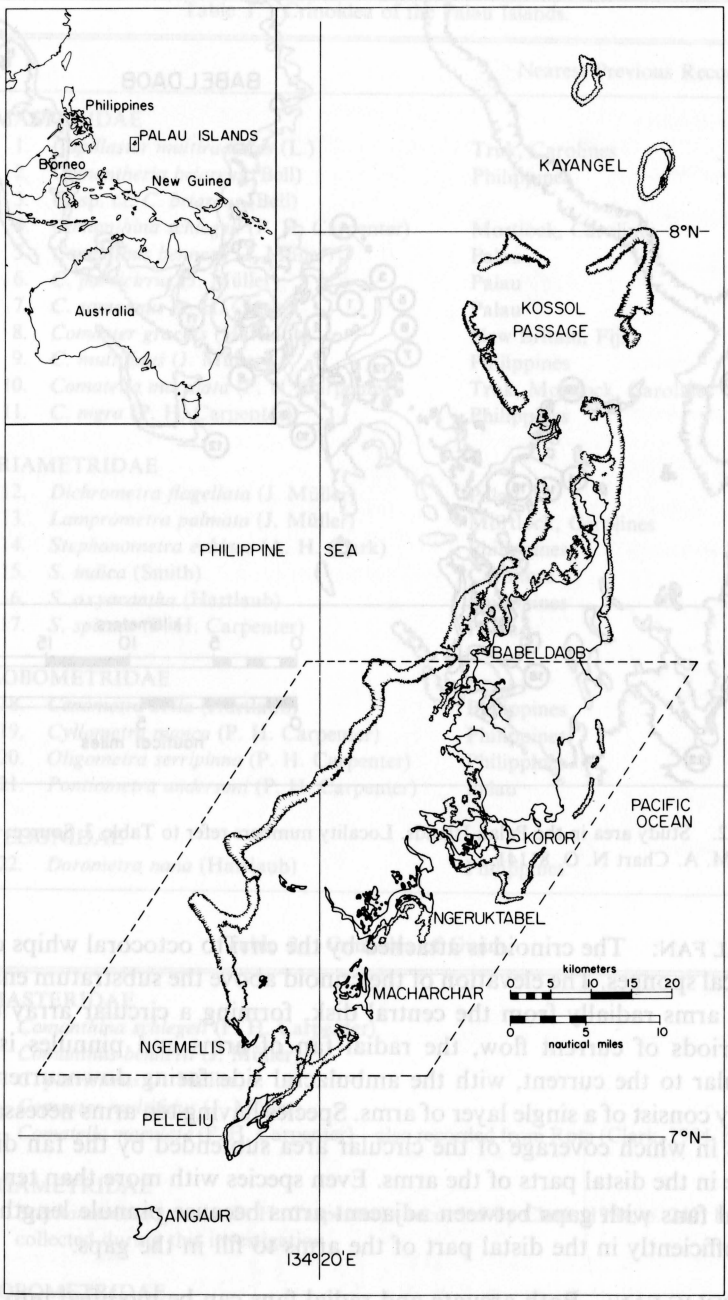

Fig. 1. The Palau Islands, Western Caroline Group. Study area bounded by dashed lines. Source: D. M. A. Chart N. O. 81141.

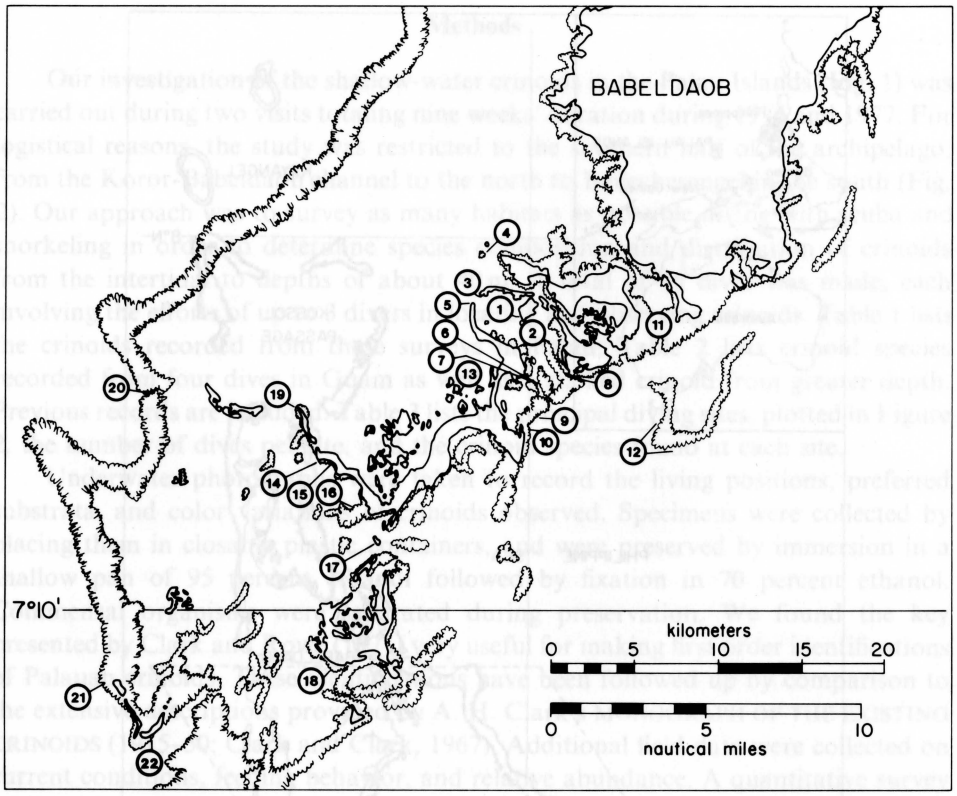

Fig. 2. Study area in the Palau Islands. Locality numbers refer to Table 3. Source: D. M. A. Chart N. O. 81141.

2) RADIAL FAN: The crinoid is attached by the cirri to octocoral whips or fans or to cylindrical sponges. The elevation of the crinoid above the substratum enables it to extend the arms radially from the central disk, forming a circular array (Fig. 3b). During periods of current flow, the radial fan of arms and pinnules is oriented perpendicular to the current, with the ambulacral side facing downcurrent. Radial fans usually consist of a single layer of arms. Species having ten arms necessarily form radial fans in which coverage of the circular area subtended by the fan diameter is incomplete in the distal parts of the arms. Even species with more than ten arms will form radial fans with gaps between adjacent arms because pinnule length does not increase sufficiently in the distal part of the arms to fill in the gaps.

3) PARABOLIC FAN: Both arcuate and radial fans can be modified into parabolic fans by curvature of the arms toward the abambulacral side. Parabolic fans are oriented with the concave side of the parabola toward the upcurrent side, retaining the downcurrent orientation of the ambulacra. In some species, the parabola lies in a concave-downward position during slack current periods, but assumes a horizontal

Table 1. Crinoidea of the Palau Islands.

	Nearest Previous Record
COMASTERIDAE	
1. *Capillaster multiradiatus* (L.)	Truk, Carolines
2. *Comantheria briareus* (Bell)	Philippines
3. *C.* sp. cf. *C. briareus* (Bell)	
4. *Comanthina schlegeli* (P. H. Carpenter)	Mortlock, Carolines
5. *Comanthus bennetti* (J. Müller)	Palau
6. *C. parvicirrus* (J. Müller)	Palau
7. *C. samoanus* A. H. Clark	Palau
8. *Comaster gracilis* (Hartlaub)	New Britain, Fiji
9. *C. multifidus* (J. Müller)	Philippines
10. *Comatella maculata* (P. H. Carpenter)	Truk, Mortlock, Carolines
11. *C. nigra* (P. H. Carpenter)	Philippines
MARIAMETRIDAE	
12. *Dichrometra flagellata* (J. Müller)	Palau
13. *Lamprometra palmata* (J. Müller)	Mortlock, Carolines
14. *Stephanometra echinus* (A. H. Clark)	Philippines
15. *S. indica* (Smith)	Carolines
16. *S. oxyacantha* (Hartlaub)	Philippines
17. *S. spicata* (P. H. Carpenter)	Palau
COLOBOMETRIDAE	
18. *Cenometra bella* (Hartlaub)	Philippines
19. *Cyllometra manca* (P. H. Carpenter)	Philippines
20. *Oligometra serripinna* (P. H. Carpenter)	Philippines
21. *Pontiometra andersoni* (P. H. Carpenter)	Palau
ANTEDONIDAE	
22. *Dorometra nana* (Hartlaub)	Philippines

Table 2. Crinoidea of Guam.

COMASTERIDAE
1. *Comanthina schlegeli* (P. H. Carpenter)
2. *Comanthus bennetti* (J. Müller)
3. *C. parvicirrus* (J. Müller)
4. *Comaster multifidus* (J. Müller)
5. *Comatella maculata* (P. H. Carpenter)—also recorded from Rota (Clark, 1954, p. 249)

MARIAMETRIDAE
6. *Stephanometra spicata* (P. H. Carpenter)—recorded by Clark (1954, p. 249) but not collected during this investigation

COLOBOMETRIDAE
7. *Cenometra bella* (Hartlaub)

ISOCRINIDAE
8. *Metacrinus nobilis* (P. H. Carpenter)

Table 3. Distribution of Palauan shallow-water crinoids.

Localities	Number of dives	*Capillaster multiradiatus*	*Comantheria briareus*	*C.* sp. cf. *C. briareus*	*Comanthina schlegeli*	*Comanthus bennetti*	*C. parvicirrus*	*C. samoanus*	*Comaster gracilis*	*C. multifidus*	*Comatella maculata*	*C. nigra*	*Dichrometra flagellata*	*Lamprometra palmata*	*Stephanometra echinus*	*S. indica*	*S. oxyacantha*	*Cenometra bella*	*Oligometra serripinna*	*Pontiometra andersoni*	*Dorometra nana*	Total species
Malakal Island,																						
1. PMRI	12	×					×			×			×	×	×		×			×		8
2. S end	2	×				×	×			×	×			×			×	×	×	×	×	11
Ngargol Island,																						
3. Bedulyaus Reef	9	×	×			×	×		×	×				×			×	×	×	×	×	12
4. Rmegethu Island	1					×								×		×						3
Ngeruktabel Island,																						
5. Kuabsngas Reef	3	×			×	×	×			×				×			×	×	×	×		10
Ngederrak Channel,																						
6. Marker 7	10	×				×	×	×	×	?	×			×			×	×		×	×	11
7. Marker 10	6				×	×	×			×				×			×	×		×		8
8. Ngel Channel	1					×	×											×		×		4
9. SW of Malakal Pass	1				×	×	×	×	×													5
10. "Whiteface Reef"	3					×	×	×		×	×			×								6
11. Koror/Babedaob Channel, S. entrance	2		×		×	×	×	×	×								×	×		×	×	10
12. Uchelbeluu Reef, Mutremdiu	16				×	×	×		×	?	×	×		×			?	×	×		×	10
13. Baitgrounds Islands, entrance to marine lake	2												×	×			×					3
Ngeruktabel Island,																						
14. W tip	5		×		×	×	×		×	×		×	×	×			×	×	×	×	×	14
15. SW bay	1		×				×										×			×		4
16. S tip	3		×		×	×	×			×	×						×	×	×	×		10
17. "Seven Beaches"	1		×			×	×										×	×	×	×		7
18. Eil Malk	1					×	×										×	×		×		5
19. Ngobasangel Island	1		×		×	×	×													×		5
20. Ulong Pass	2		×			×	×	×	×		×			×			×	×			×	10
Ngemelis Islands,																						
21. Arimasuku Island	2								×									×				2
22. Bailechesengel Is.	10		×	×	×	×	×	×	×	?				×			×	×	×	×	×	13

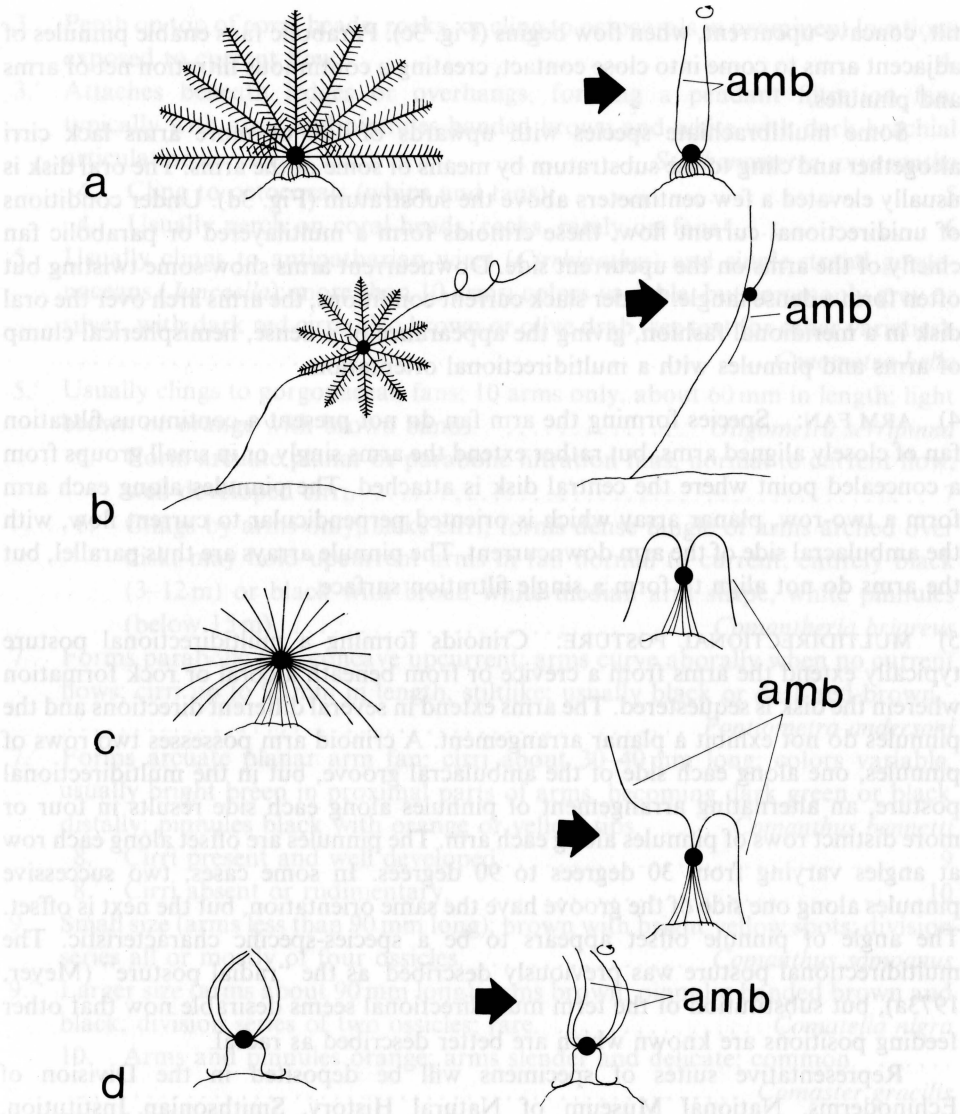

Fig. 3. Diagrammatic sketches of the principal modes of filtration fan formation by comatulid crinoids. a. Arcuate fan. Left, view parallel to current direction; right, view perpendicular to current direction (large arrow); small arrow indicates twisting of downcurrent arms so that food grooves are downcurrent. b. Radial fan. Left, view parallel to current direction with crinoid attached to wire coral; right, view perpendicular to current direction (large arrow), with food grooves downcurrent. c. Parabolic fan. Right, top, view of crinoid with elongate cirri during slack current; below, view of same crinoid with current from left, showing uplift of arms on upcurrent side. Note that food grooves are downcurrent. Left, view downcurrent toward concavity of parabolic fan, with pinnules omitted. d. Arm postures of multibrachiate species that lack cirri. Left, view of meridional posture of arms during slack current; note elevation of calyx by arms; right, view of parabolic fan oriented to current from left.

tilt, concave-upcurrent, when flow begins (Fig. 3c). Parabolic fans enable pinnules of adjacent arms to come into close contact, creating a continuous filtration net of arms and pinnules.

Some multibrachiate species with upwards of 100 or more arms lack cirri altogether and cling to the substratum by means of some of the arms. The oral disk is usually elevated a few centimeters above the substratum (Fig. 3d). Under conditions of unidirectional current flow, these crinoids form a multilayered or parabolic fan chiefly of the arms on the upcurrent side. Downcurrent arms show some twisting but often form a dense tangle. Under slack current conditions, the arms arch over the oral disk in a meridional fashion, giving the appearance of a dense, hemispherical clump of arms and pinnules with a multidirectional orientation.

4) ARM FAN: Species forming the arm fan do not present a continuous filtration fan of closely aligned arms, but rather extend the arms singly or in small groups from a concealed point where the central disk is attached. The pinnules along each arm form a two-row, planar array which is oriented perpendicular to current flow, with the ambulacral side of the arm downcurrent. The pinnule arrays are thus parallel, but the arms do not align to form a single filtration surface.

5) MULTIDIRECTIONAL POSTURE: Crinoids forming a multidirectional posture typically extend the arms from a crevice or from beneath a coral or rock formation wherein the disk is sequestered. The arms extend in several different directions and the pinnules do not exhibit a planar arrangement. A crinoid arm possesses two rows of pinnules, one along each side of the ambulacral groove, but in the multidirectional posture, an alternating arrangement of pinnules along each side results in four or more distinct rows of pinnules along each arm. The pinnules are offset along each row at angles varying from 30 degrees to 90 degrees. In some cases, two successive pinnules along one side of the groove have the same orientation, but the next is offset. The angle of pinnule offset appears to be a species-specific characteristic. The multidirectional posture was previously described as the "radial posture" (Meyer, 1973a), but substitution of the term multidirectional seems desirable now that other feeding positions are known which are better described as radial.

Representative suites of specimens will be deposited in the Division of Echinoderms, National Museum of Natural History, Smithsonian Institution, Washington, D. C., and at the Marine Laboratory, University of Guam.

LIFE-HABIT AND COLOR KEY TO PALAUAN CRINOIDS

1. Fully or partly visible by day. 2
1.′ Hidden by day; may be found curled up beneath coral heads or within crevices; emerge by night. 13
2. Form a filtration fan, usually fully visible. ..... 3.
2.′ Do not form filtration fan; arms only visible; pinnules have offset arrangement along arm. 8

3. Perch on top of coral heads, rocks, or cling to octocorals in prominent locations exposed to current flow. ..... 4.

3.′ Attaches beneath ledges or overhangs, forming a pendant filtration fan; typically with arms and pinnules banded brown and white with dark brachial articulations. ..... *Stephanometra oxyacantha*

4. Cling to octocorals (whips and fans). 5

4.′ Usually perch on coral heads, rocks, rarely on fans[a]. 6

5. Usually clings to antipatharian wires (*Cirrhipathes*) and single-strand gorgonaceans (*Junceella*); more than 10 arms; colors variable, but commonly grey or silver, with dark red cirri; also brown or olive drab (see text for other varieties). ..... *Cenometra bella*

5.′ Usually clings to gorgonacean fans; 10 arms only, about 60 mm in length; light brown or orange with brown bands. ..... *Oligometra serripinna*

6. Form arcuate planar or parabolic filtration fans, normal to current flow; well developed cirri. 7

6.′ Clings by arms only; lacks cirri; forms dense tangle of arms arched over disk; may hold upcurrent arms in fan normal to current; entirely black (3–12 m) or black with broad white median arm stripe, white pinnules (below 15 m). ..... *Comantheria briareus*

7. Forms parabolic fan, concave upcurrent; arms curve aborally when no current flows; cirri up to 90 mm in length, stiltlike; usually black or dark red-brown. ..... *Pontiometra andersoni*

7.′ Forms arcuate planar arm fan; cirri about 30–40 mm long; colors variable, usually bright breen in proximal parts of arms, becoming dark green or black distally; pinnules black with orange or yellow tips. .... *Comanthus bennetti*

8. Cirri present and well developed 9

8.′ Cirri absent or rudimentary. 10

9. Small size (arms less than 90 mm long); brown with bright yellow spots; division series all or mostly of four ossicles. ..... *Comanthus samoanus*

9.′ Larger size (arms about 90 mm long); arms brown, pinnules banded brown and black; division series of two ossicles; rare. ..... *Comatella nigra*

10. Arms and pinnules orange; arms slender and delicate; common. ..... *Comaster gracilis*

10.′ Not as above 11

11. Arms banded white, black, and yellow, pinnules black or white with yellow tips (see text for other varieties); often large, with 100 or more arms; on each ray, external IIIBrr of two ossicles, internal IIIBrr of four ossicles. ..... *Comanthina schlegeli*

11.′ Colors not as above. 12

12. Arms usually orange, pinnules black or dark purple; some or all arms may be entirely yellow, green, or black; usually concealed by day within branching coral thickets; arm branches paired with free arms. ..... *Comaster multifidus*

12.′ Arms long and delicate but less so than in *Comaster gracilis*; central disk hidden within crevices or beneath corals, arms extending; colors highly variable, but often with dark brachial articulations appearing as transverse bands; arms may be green, with red pinnules; arms may also be dark grey, black, yellow, or mottled green and brown; division series all or mostly of four ossicles. ..... *Comanthus parvicirrus*

13. Form a filtration fan; may be entirely visible or partly concealed. 14

13.′ Feeding position unknown but presumably nocturnal. 18

14. Extends arms from a concealed position, with pinnules in a planar array but arms not closely positioned; variegated red and white or entirely dark red. ..... *Capillaster multiradiatus*

14.′ Perch on prominent positions, entirely visible. 15

15. Possess spikelike oral pinnules. 16

15.′ Oral pinnules not spikelike. 17

16. Arms and pinnules banded brown and white, with dark brachial articulations; up to five spikelike oral pinnules per arm; cirri lack spines. ..... *Stephanometra oxyacantha*

16.′ Arms and pinnules golden or red-orange; forms a parabolic filtration fan; possesses distinct spines on cirri. ..... *Stephanometra echinus*

17. Arms and pinnules usually banded green and white in various patterns, but may also be banded with brown or orange and white .... *Lamprometra palmata*

17.′ Never green; arms and pinnules usually banded with purple and white or brown and white; proximal arm sections white, pink, or grey with purple articulations. ..... *Dichrometra flagellata*

18. Solid dark red in color; well developed cirri; about 20 arms; flexible, comb-bearing oral pinnules; crawls rapidly. ..... *Comatella maculata*

18.′ Not as above. 19

19. Capable of swimming by rapid arm flexion[b]; 10 arms; small and delicate. ..... *Dorometra nana*

19.′ Variable in color; may be banded red and white, solid reddish purple or pink; only the second oral pinnule is spikelike. ..... *Stephanometra indica*[c]

Notes: a—*Comanthus bennetti* may attach to fans below 15 m where it occurs as a grey form with pinnules white or black with yellow tips.

b—*Dorometra nana* is the most active swimmer among the Palauan crinoids; other swimming species are less prone to swimming when disturbed than *D. nana*.

c—*Stephanometra spicata* is not included in this key because the species was not observed during this study although it has been reported from Palau.

Fig. 4a. *Comantheria* sp. cf. *C. briareus* forming multilayered filtration fan normal to current flowing from left. Bailechesengel Island; depth 23 m, on *Porites lutea* colony projecting from vertical wall. Note lower arms used in clinging to coral. Arm length about 14 cm.

4b. *Comanthus bennetti.* Bailechesengel Island; depth 6 m along edge of vertical wall. Arm length 15–20 cm.

4c. *Comanthus bennetti*, showing deflection of arms of mutilayered filtration fan by current from right. Koror-Babeldaob Channel; depth 3 m. Arm length 15–20 cm.

4d. *Comanthus bennetti*, showing three color varieties and arm posture assumed during slack current conditions. Arm length 15–20 cm.

4e. *Comanthus bennetti*, showing color variety found along deep fore-reef environment. Bailechesengel Island; depth 15–23 m. Arm length 15–20 cm.

4f. *Comanthus parvicirrus*, showing multidirectional posture of arms and pinnules. Note offset of pinnules along each side of an arm and curvature of pinnules. Near western tip of Ngeruktabel; depth about 5 m. Pinnule length about 6 mm.

4g. *Comanthus parvicirrus* (right, green arms, red pinnules) and *Comaster gracilis* (left, orange arms and pinnules). Bailechesengel Island. Arm length of *C. parvicirrus* about 15 cm.

4h. *Comaster gracilis*, showing section of one arm with offset pattern of pinnules and arrangement of tube feet along pinnules. Northern tip of Ngeruktabel. Pinnule length 10 mm.

Fig. 5a. *Dichrometra flagellata,* photographed at 1910 hrs., forming arcuate filtration fan normal to current flowing into photograph. Reef off PMRI, Malakal Harbor; depth 2–3 m. Arm length about 17 cm.

5b. *Dichrometra flagellata*, photographed at about 2100 hrs. Reef off PMRI, Malakal Harbor; depth 2–3 m. Pinnule length about 10 cm.

5c. *Lamprometra palmata* (above, green and white), forming filtration fan normal to current from the rear; *Capillaster multiradiatus* (center, red and white), forming arm fan. Photographed at about 1930 hrs. Reef off PMRI, Malakal Harbor; depth 2–3 m. Arm length of *L. palmata* about 10 cm.

5d. *Lamprometra palmata*, photographed at about 1810 hrs., forming arcuate filtration fan normal to current flowing into photograph. Reef off PMRI, Malakal Harbor; depth 2–3 m. Arm length about 10 cm.

5e. *Stephanometra echinus*, photographed at night. Note elongate oral pnnules forming spike-like palisade over oral disk. Reef off PMRI, Malakal Harbor; depth 3 m. Distal pinnule length about 9 mm.

5f. *Cenometra bella.* Pair of individuals with contrasting color patterns clinging to wire coral. Bedulyaus Reef, Ngargol Island; depth about 3 m. Pinnule length about 9 mm.

5g. *Cenometra bella*, showing cirri, division series, and proximal arms. Bedulyaus Reef, Ngargol Island; depth 3–5 m. Arm width 1.5 mm.

5h. *Pontio etra andersoni*, forming parabolic filtration fan concave toward current flowing into photograph. Ngederrak Channel; depth about 4 m. Arm length about 12 cm. Note upraised cirri.

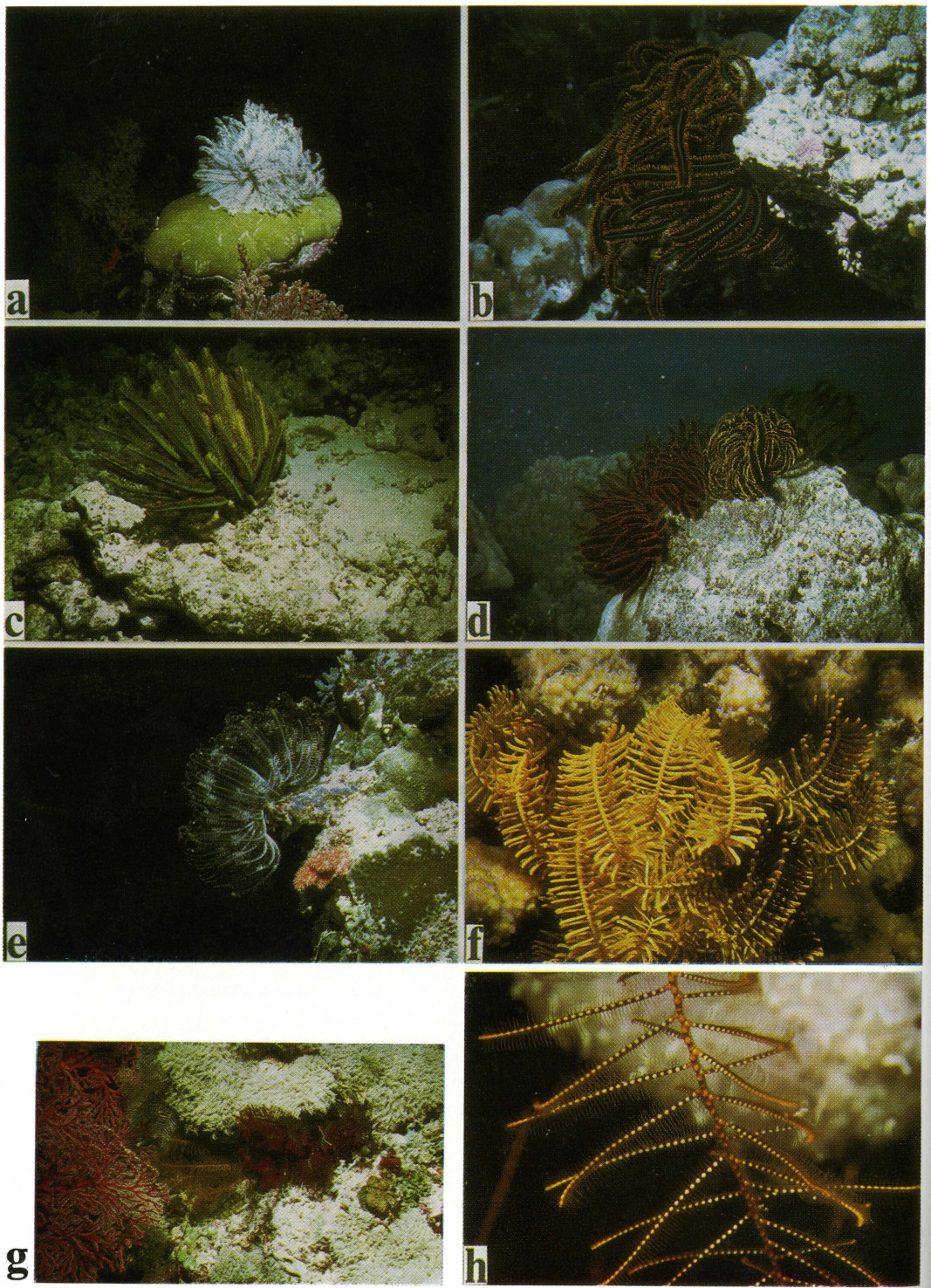

Fig. 4.

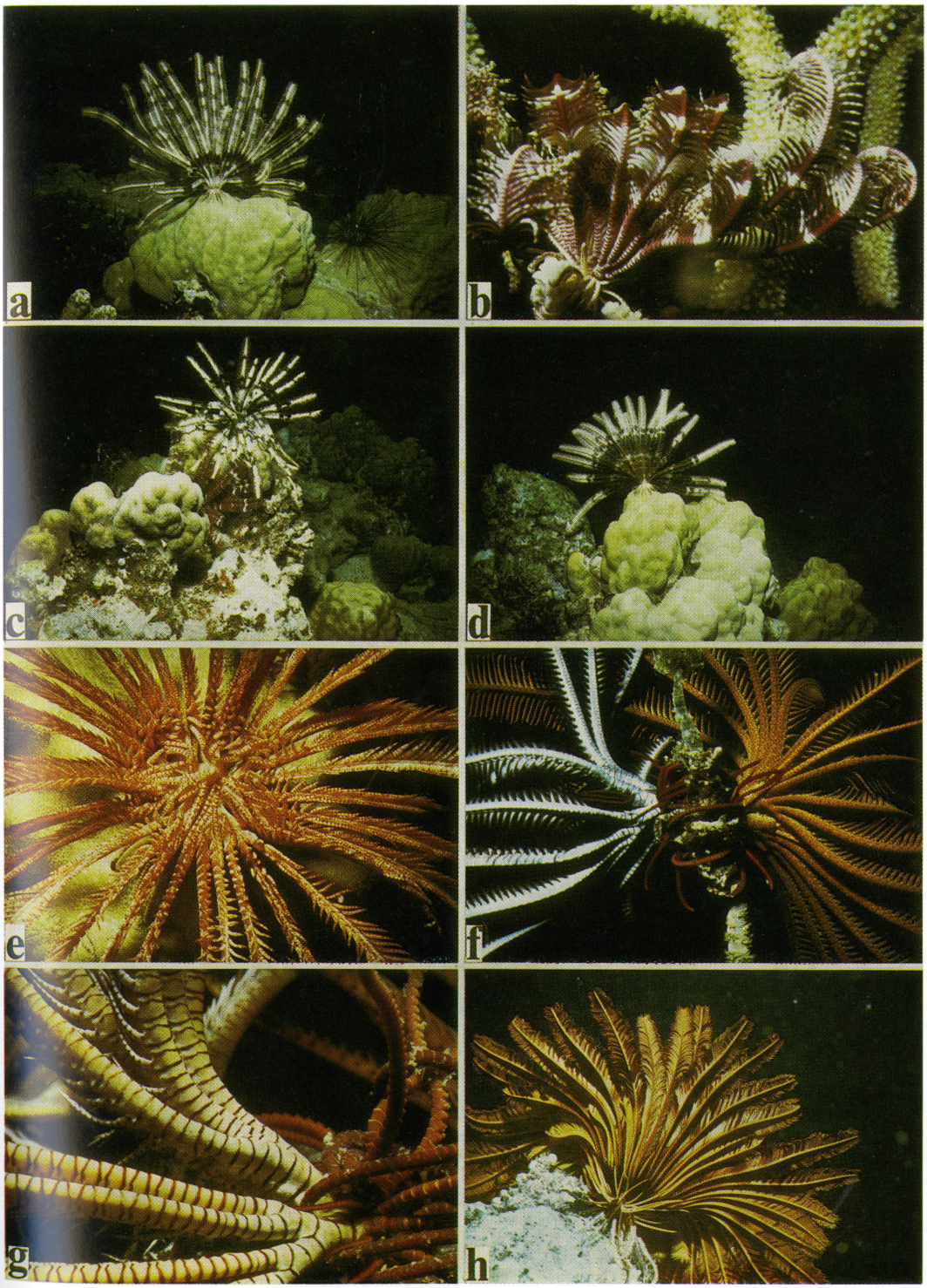

Fig. 5.

Fig. 6a. *Capillaster multiradiatus* extending arms from clump of *Porites andrewsi* at night. Reef off PMRI, Malakal Harbor; depth 2–3 m. Arm length about 15 cm.

6b. *Comantheria* sp. cf. *C. briareus* forming multilayered filtration fan normal to current flowing into photograph. Bailechesengel Island; depth about 16 m. along vertical wall. Note lower arms used in clinging to rock. Arm length about 14 cm.

6c. *Comantheria* sp. cf. *C. briareus*. Aboral side, showing black and white color pattern, centrodorsal, division series, and proximal arms. Bailechesengel Island; depth, below 15 m. Width of proximal arms about 3 mm.

6d. *Comanthina schlegeli* with arms extended in arcuate fan normal to current flowing into photograph. Ngederrak Channel; depth 3 m. Arm length about 15 cm.

6e. *Comanthus bennetti*. Cluster forming arcuate fans normal to tidal current from right. Koror-Babeldaob Channel; depth 2–3 m. Arm length 15–20 cm.

6f. *Comanthus bennetti*, with arms deflected by current from left. Koror-Babeldaob Channel; depth 2–3 m. Arm length 15–20 cm.

6g. *Comanthus parvicirrus*. Aboral view showing pentagonal centrodorsal bearing a single cirrus, division series and arms with typical dark articulations. Near western tip of Ngeruktabel. Centrodorsal diameter about 3 mm.

6h. *Comaster gracilis*. Aboral view showing stellate centrodorsal with no cirri, division series, proximal arms, and visceral mass visible in interbrachial angles. Bedulyaus Reef, Ngargol Island. Centrodorsal diameter about 2 mm.

Fig. 7a. *Lamprometra palmata*, showing chevron patterns (green) on white background. Arms extended at night. Reef of PMRI, Malakal Harbor; depth 2–3 m. Pinnule length about 7 mm.

7b. *Stephanometra echinus* forming filtration fan, perched on *Porites lutea* at night. Current from left. Reef off PMRI, Malakal Harbor; depth 3–4 m. Arm length about 17 cm.

7c. *Stephanometra oxyacantha*, photographed by day, forming pendant arcuate filtration fan within reef infrastructure. Color white with brown bands. Ulong Pass; depth about 10 m. Arm length about 12 cm.

7d. *Cenometra bella*. Cluster attached to wire coral. Bedulyaus Reef, Ngargol Island; depth 4–5 m. Arm length about 12 cm.

7e. *Cenometra bella*. Oral side showing palisade over oral disk formed by elongated second pinnules. Bedulyaus Reef, Ngargol Island. Length of elongated oral pinnules about 7 mm.

7f. *Oligometra serripinna*, clinging to gorgonacean fan. Bedulyaus Reef, Ngargol Island; depth about 14 m. Pinnule length about 3 mm.

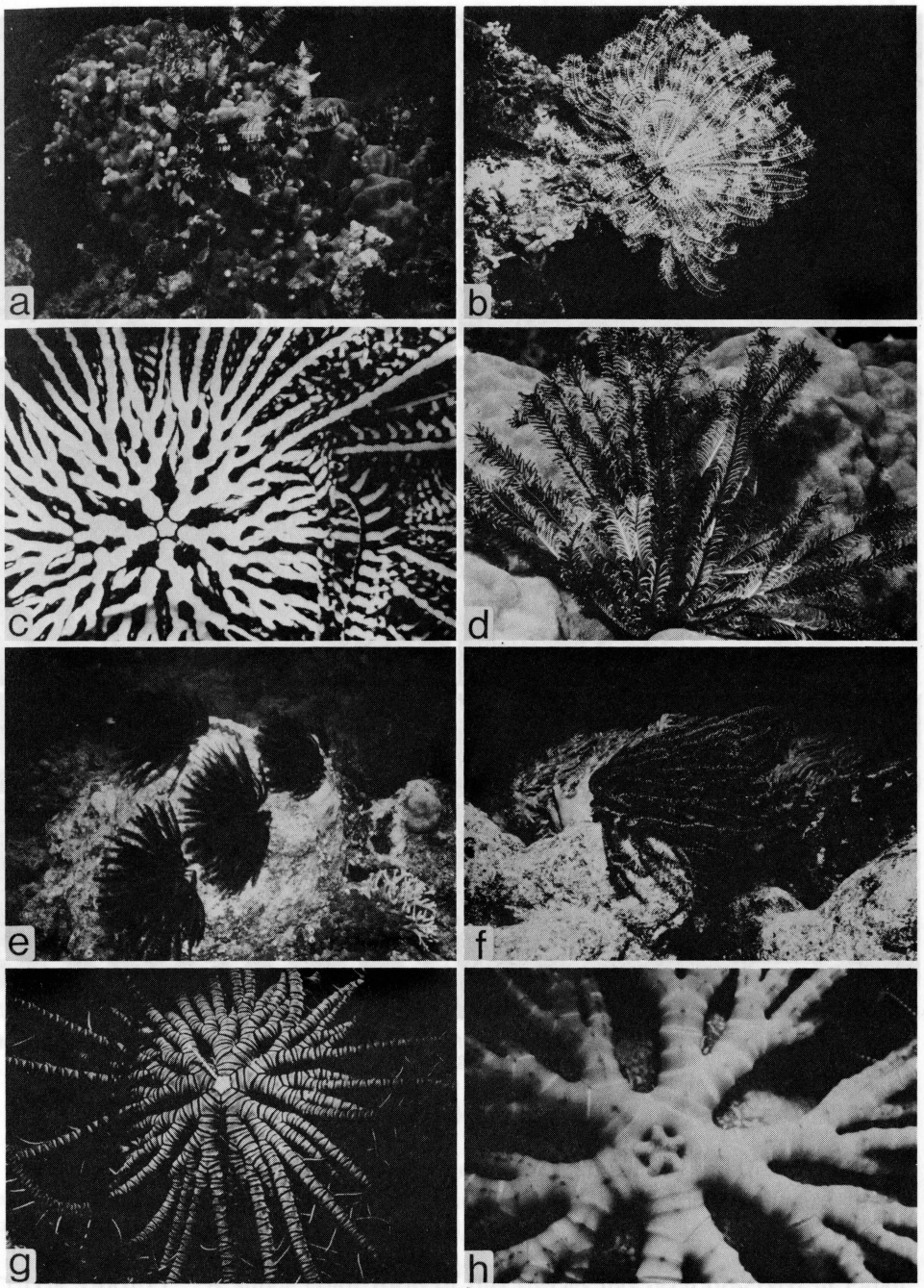

Fig. 6.

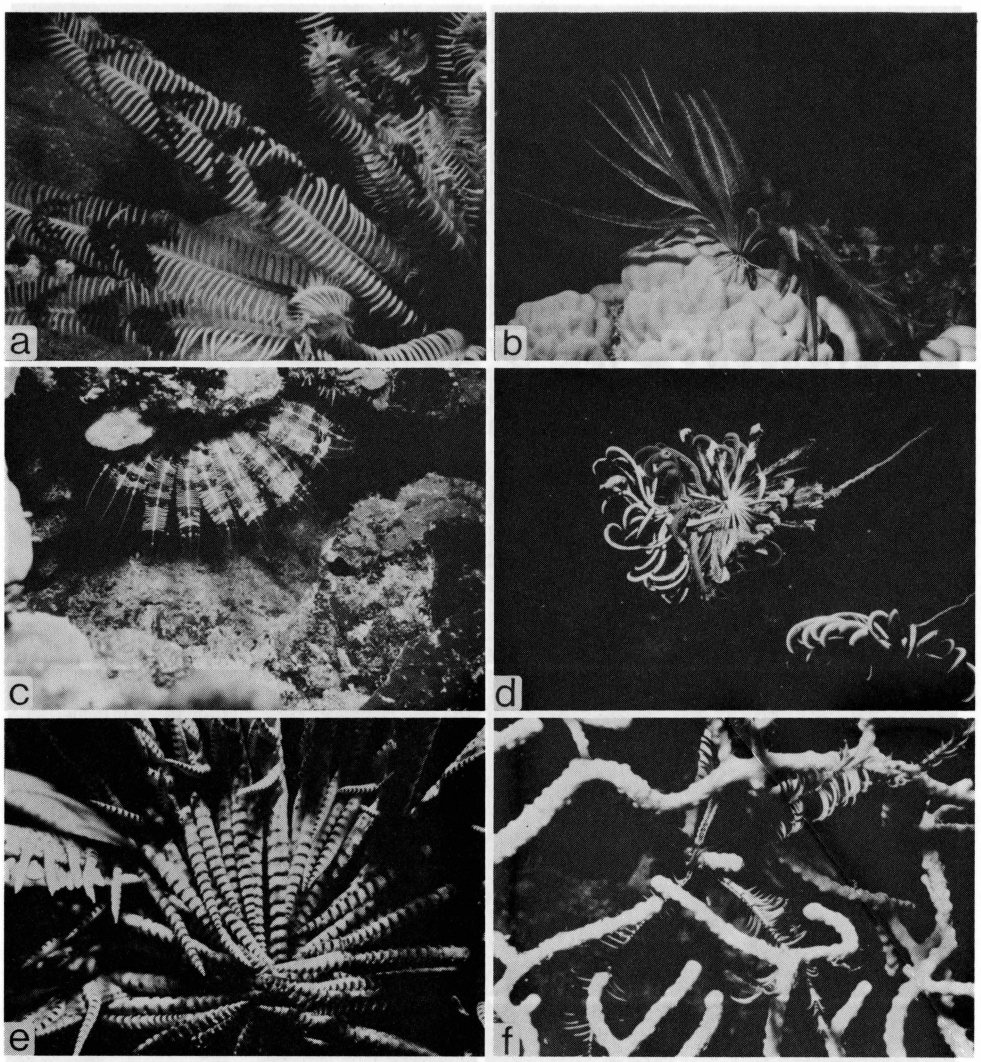

Fig. 7.

Systematic Account

Capillaster multiradiatus (L.)

Hartlaub (1891, cited in Clark, 1931, p. 203) first reported *C. multiradiatus* from Truk, Caroline Islands.

COLOR VARIETIES: This crinoid exhibits a wide range of color variation, from solid red individuals to ones having varying proportions of red and white (Fig. 5c). Arms and pinnules can show even red and white bands, or can be white with red spots in proximal or middle sections and solid red distally. The cirri are banded red and white; the pinnules are solid red or white, usually where arm color is solid, or they have narrow red and white bands. The red pigmentation varies from light to dark, occasionally appearing brown or yellowish.

OCCURRENCE: The distribution of *C. multiradiatus* as listed in Table 3 is probably not indicative of the actual occurrence of this crinoid in the area studied. Its great abundance at Malakal Island, the only locality where night diving was done, suggests that this species is widely distributed in the Palau Islands. At Malakal, *C. multiradiatus* was found at depths of 2–3 m.

LIFE HABITS: At Malakal Island, *Capillaster multiradiatus* is the dominant member of the nocturnal crinoid fauna, while it is completely hidden by day. It emerges by night from crevices within massive heads of *Porites lutea*, from thickets of branching coral, or from beneath other corals (Figs. 5c, 6a). The pinnules form a planar array along each arm (arm fan) which is oriented normal to the current direction with the ambulacral groove downcurrent. The arms are not arranged contiguously to form a true filtration fan although arm fans of the several exposed arms are parallel. The pinnules curve toward the abambulacral side of the arm.

The nocturnal emergence of *C. multradiatus* commences about one hour before sunset and is essentially complete by sunset. The retreat at daybreak begins well before the sun is above the horizon. At Malakal Island where the retreat was observed during dawn dives, steep hills along the shore blocked the view of the sunrise, but by about 0615 (during August) most *Capillaster* were concealed. On some overcast days a few individuals were emergent during daylight hours.

Comantheria briareus (Bell)

This is the first record of this species from the Palau Islands and the Carolines. It was previously reported "from Java to northern Australia and northward to the Philippines and Formosa" (Clark, 1931, p. 502).

COLOR VARIETY: A single color form of this species has been observed in Palau: arms and pinnules solid black; pinnules can have yellow tips.

OCCURRENCE: Table 3 shows that *C. briareus* was found more frequently toward

the southern part of the area examined. It was particularly common near the weastern tip of Ngeruktabel where aggregations of several individuals were found on single coral formations. The sites where it was found are well exposed to currents.

LIFE HABITS: This crinoid is typically seen fully exposed to view, perched on corals or soft corals. The arms are held in a meridional array, arching downward from the calyx then up and over the oral disk (Fig. 3d). Cirri are totally lacking and the crinoid is attached by the pinnules along the median or distal parts of the arms. The calyx is actually raised up above the substratum as much as 4 cm. The pinnules may be held in a multidirectional array or else infolded along the arms; nevertheless the tube feet can be extended. On one occasion a pair of *C. briareus* was observed on the reef slope at the northern entrance to Malakal Harbor at a depth of about 10 m. These crinoids were forming a common filtration fan toward a tidal current from the south. Arms on the downcurrent side were twisted to achieve the characteristic orientation of fan-forming crinoids. While this species is found as single individuals, aggregations of several individuals were observed along the southwest side of Ngeruktabel. As this population was not observed in the fan-forming mode, it is not known whether or not multiple common filtration fans are formed by this species. The regenerative abilities of this species were demonstrated following removal of the visceral masses from two individuals. Apparent complete regeneration of the oral disk occurred within 18 days.

Comantheria sp. cf. *C. briareus*

The color patterns and occurrence of this crinoid are so distinct from specimens described above as *C. briareus* that the two appear to be distinct species. However, morphologically both forms conform to the description of *C. briareus* given by Clark (1931, p. 493 ff). In both, the tertibrachs are made up of two ossicles (occasionally four), and the succeeding division series consist of four ossicles. This eliminates both *C. polycnemis* and *C. alternans* from consideration as both species have some division series beyond the tertibrachs of two ossicles (Clark 1931, p. 484). *C. briareus* remains as the only other described species of *Comantheria* which lacks cirri and has over 40 arms. Specimens here referred to *C.* sp. cf. *C. briareus* have over 100 arms up to 140 mm in length, while those referred to *C. briareus* are smaller, with over 80 arms up to 100 mm in length. Both fall within the range of variation for *C. briareus* indicated by Clark. In *C.* sp. cf. *C. briareus* the number of poximal pinnules bearing comb teeth is greater than in specimens referred to *C. briareus* and the form of the comb teeth also differs between the two. Further examination of Palauan material and Australian material which presents a similar dilemma will be necessary before the nature of the variants described here can be conclusively determined. According to the existing taxonomy, both forms fall within the limits of *C. briareus*, but we believe there is a strong likelihood that further research will lead to discrimination of the two at the species level.

This crinoid has been found at a single locality in the Palau Islands, along the

vertical wall of the "Great Reef" (see Faulkner, 1974) at Bailechesengel Island, at depths below 15 m. It was not found along a comparable vertical wall at Arimasuku Island just to the north of Bailechesengel, where the fore-reef escarpment faces directly westward into the Philippine Sea. It was not found along another vertical wall at Mutremdiu, on the Pacific Ocean side of the archipelago. At Bailechesengel, this crinoid is quite common, with up to about a dozen individuals sighted on a single dive between 15 and 22 meters.

COLOR VARIETIES:

1. arms black; pinnules white.
2. arms with wide white median band, flanked by black; pinnules mostly white with some narrow black bands; arms may become black toward tips (Figs. 4a, 6b, c).
3. arms and pinnules solid white; interradial areas of division series and ambulacra black.

LIFE HABITS: Although *Comantheria* sp. occurs in a quite different habitat than *C. briareus*, the living habits of the two species appear to be similar. *Comantheria* sp. attaches by the arms and pinnules so that the calyx is elevated above the substratum. It occupies prominent projecting points along the vertical wall (Figs. 4a, 6b), and generally appears as a dense tangle of arms held in a meridional posture. However, under conditions of current flow along the wall, *Comantheria* sp. forms a filtration fan of the arms on the upcurrent side at least (Fig. 4a). This fan may be planar or parabolic with the concave side upcurrent. Arms on the downcurrent side remain in a dense ball. *Comantheria* sp. usually occurs as single individuals but on one occasion two were found side by side. The pinnules show a slight multidirectional posture.

Comanthina schlegeli (P. H. Carpenter)

Comanthina schlegeli was reported from Mortlock Island, Carolines, in 1891 by Hartlaub (cited in Clark, 1931, p. 479).

COLOR VARIETIES:

1. cirri and centrodorsal white with occasional black aboral spots on cirri, cirri with yellow tips; division series variegated white, black, and yellow; arms banded black and yellow, with some white sections; pinnules black with yellow tips or white with yellow tips.
2. cirri white; arms orange; pinnules brown with white tips.
3. arms yellow-green; pinnules dark green with yellow tips.

OCCURRENCE: This species is not common in Palau, but was found at most sites where there is exposure to currents. Two sites where more than one or two individuals were found were the Koror-Babeldaob Channel and Mutremdiu (Table 3).

LIFE HABITS: Unlike its characteristic appearance elsewhere in the Indo-West Pacific, *Comanthina schlegeli* in Palau is found extending the arms from recesses in the

reef, usually from between coral heads. In Guam, *C. schlegeli* is completely exposed on coral or rock surfaces, its more typical mode of life. Attachment is solely by means of the arms as the cirri are few in number or lacking altogether. Under conditions of tidal current flow in Palau, *C. schlegeli* extends the arms in a multilayered filtration fan normal to the flow direction, while the animal remains attached within its crevice (Fig. 6d). The arms are loosely coiled when flow ceases. The pinnules are held in a multidirectional array similar to that of other comasterids, with an acute angle of offset between pinnular rows and pinnular curvature toward the abambulacral side of the arm. No information is available on the possibility of nocturnal emergence in this species.

Comanthus bennetti (J. Müller)

Comanthus bennetti is probably the most conspicuous and widespread of the Palauan crinoids. It was first reported from Palau in 1877 by Lütken (Clark, 1931, p. 543, listed as "Pelew Islands"). Specimens collected during the present study conform well with the description given by Clark (1931, p. 534).

COLOR VARIETIES: The following color varieties were found in the Palauan population of *C. bennetti.*

1. cirri golden brown, green, or yellow-green; centrodorsal and division series speckled bright green; arms green, often appearing black; pinnules black with orange or yellow tips (Figs. 4b, d).
2. arms and pinnules banded black, with distal edges green; pinnules with orange tips, or orange may cover distal half of pinnules (Figs. 4c, d).
3. division series yellow; free arms green except for some yellow sections having yellow pinnules; pinnules otherwise green.
4. cirri white; arms grey; pinnules white or black, sometimes with yellow tips; distal pinnules may be entirely yellow (Fig. 4e).

The fourth color variety is found only below depths of about 15 m, while the others are found as shallow as 2–3 m.

OCCURRENCE: Table 3 shows that this species occurs at more diving stations than any other species in Palau. A true rheophilic crinoid, *C. bennetti* is always found at sites where currents regularly flow. Thus, the largest populations are found along the edges of the narrow passes which channel tidal flow in and out of the archipelago (Fig. 6e). The heaviest aggregations occur where salients extend into the channel, accentuating current velocities. Over 100 individuals were counted over a distance of about 400 m along the northeast side of Ngel Channel off Ngeruptachel Island. A similar microdistributional effect was observed along the southwest limb of Ngeruktabel, where the species is restricted to projecting promontories but is absent from the intervening embayments. *C. bennetti* is also abundant along the edge of the fore-reef escarpment of Mutremdiu, where it is restricted to depths of about 5–10 m, with the exception of a single individual of the gray color variety found at about 40 m.

A similar "edge effect" was seen along the Great Reef at Bailechesengel, where the deeper form was quite common below about 15 m. Along the western, open-sea side of the Ngemelis Group, this species was not found within the range 0–30 m, possibly a consequence of frequent heavy wave surge along that side.

LIFE HABITS: *Comanthus bennetti* attaches by the cirri to prominent coral formations, rocks, or octocorals which are well exposed to current flow. The entire animal is exposed to view. Juveniles have been observed attached within small caves or beneath overhangs. This species is a typical fan former, and exhibits feeding postures very similar to those described for *Nemaster grandis* Clark in the Caribbean by Meyer (1973a). The two species are partial ecological equivalents. Although *C. bennetti* occurs where current flow is frequent, slack currents occur during tidal reversals. At these times, the arms are held arched over the disk in a meridional arrangement or else verticallly with the distal tips incurved (Fig. 4d). The pinnules are held in a four-row offset arrangement along each arm. This behavior is very similar to that found in *N. grandis* under similar conditions.

Under very slight current velocities *C. bennetti* forms the arms into an arcuate filtration fan oriented normal to the flow direction. As flow begins, arms on the downcurrent side of the fan have the good grooves oriented upcurrent, but these arms soon twist so that the food grooves attain the downcurrent orientation seen in other rheophilic crinoids (Meyer, 1973a). The pinnules assume a more planar arrangement along each arm, but may still retain a slight offset pattern even when the arm fan is formed. The pinnules also become slightly curved into the current. In *N. grandis,* the pinnules are nearly planar and show no curvature under such flow conditions (Meyer, 1973a).

As tidal currents rapidly increase in velocity, the arcuate fan of *C. bennetti* becomes depressed in the downcurrent direction, as in *N. grandis* (Fig. 4c). Eventually the fan becomes deformed to the point where the arms are compressed into a cylinder oriented downcurrent like a windsock (Fig. 6f). Arms and pinnules passively "flap" during extreme conditions as in *N. grandis.* Even though *C. bennetti* has been observed under more extreme flow velocities than has *N. grandis* in the Caribbean no clear indication of the retreat to shelter has been observed in *C. bennetti* as it has in *N. grandis.* Maximum flow velocities experienced during diving in the Palauan reef passes inhabited by *C. bennetti* probably exceed two knots (100 cm/sec). It was not possible to swim against such currents with fins. *C. bennetti* appears to be tolerant of such extreme currents. On some occasions, this crinoid was observed to extend an arm to the substratum as a tether to assist the cirri in maintaining position. Recurved hooks on the distal pinnulars serve as grapnels. A few individuals were observed in a crawling posture during extreme flow conditions in abnormal positions among the corals. It is possible that occasionally some of these hardy crinoids are dislodged by the current and most regain a feeding perch by crawling. Even under extreme flow conditions, the tube feet of *C. bennetti* remain extended, so that some food capture can occur.

C. bennetti occurs singly or in aggregations of up to a dozen or two clustered on a single coral formation. In aggregations (Figs. 4d, 6e), individuals do not appear to be as closely associated as in clusters of *N. grandis* (Meyer, 1973a). *C. bennetti* does not appear to form the type of intimately overlapping common filtration fans found in *N. grandis*.

The deeper water color morph of *C. bennetti* referred to earlier has life habits similar to those observed in the shallower form. This morph occurs in exposed positions on vertical reef escarpments below about 15 m depth where it forms a filtration fan normal to flow along the reef face (Fig. 4e). This form occurs on octocorals as well as stony corals and rocky substrata. It has been observed only as single individuals.

Comanthus parvicirrus (J. Müller)

Comanthus parvicirrus is one of the most common crinoids in Palau, and is highly variable in color. The species was previously reported from Palau ("Pelew") by Clark in 1912 and from Ponape by Hartlaub in 1891 (cited in Clark, 1931). As noted by Clark (1931), this is an exceedingly variable species. Specimens from Palau agree with the general diagnosis of this species, but display considerable variation in color and morphology.

COLOR VARIETIES: The following color varieties were found in the Palauan material, although additional types may also occur.

1. arms green; pinnules red or reddish brown; pinnules can also be yellow-green with orange ambulacra (Fig. 4g).
2. arms, including centrodorsal and division series, green with black articulations (Fig. 6g); pinnules with orange tips; arms can appear brown, flecked with green, at close range.
3. arms and pinnules dark grey or black; can have yellow spots on distal edges of brachials.
4. arms, including centrodorsal and cirri, yellow, with black articulations; sometimes with black median stripe which thins through center of each brachial; oral disk, oral pinnules, and ambulacra can be blue (Fig. 4f).
5. proximal arms mottled green and brown.

OCCURRENCE: Like *Comanthus bennetti*, *C. parvicirrus* was found at practically every diving station in Palau (Table 3). It was generally found to be low in abundance except at one station, near the western tip of Ngeruktabel where an abundance and diversity of color forms was found. Its distribution in Palau is similar to that of *Nemaster rubiginosa* (Pourtalès) and *N. discoidea* (P. H. Carpenter) in the Caribbean (Meyer, 1973a), in that it is most abundant at sites well exposed to current flow, but will also occur at less well exposed sites in the absence of other more rheophilic crinoids.

LIFE HABITS: *Comanthus parvicirrus* is an inhabitant of the infrastructure of the reef. Although the disk is hidden within crevices, beneath corals or soft corals, the arms are extended conspicuously into spaces down among corals rather than atop prominences (Figs. 4f, g). Because the cirri are absent or weakly developed (Fig. 6g), attachment to the substratum is accomplished by means of some of the arms and pinnules. Except for the lack of well developed cirri, *C. parvicirrus* very closely resembles the tropical western Atlantic species *Nemaster rubiginosa* in its living position (Meyer, 1973a).

Like *N. rubiginosa*, *C. parvicirrus* does not form a filtration fan, but rather extends the arms in a multidirectional posture (Figs. 4f, g). The pinnules are held in a four-row posture, with the angle of offset of the two rows along one side of the arm being about 30 degrees (Fig. 4f). The pinnules frequently curve toward the abambulacral side of the arm.

C. parvicirrus usually occurs as single individuals and does not form dense aggregations. A pair of alpheid shrimp (*Synalpheus*) is frequently associated with this species, located on the oral disk.

Comanthus samoanus A. H. Clark

Although it is an uncommon species in Palau, *Comanthus samoanus* was reported from Palau ("Pelew Islands") by Lutken in 1877 and from Truk ("Ruk") by Clark in 1912 (cited in Clark, 1931). A single color form has been observed: cirri and centrodorsal brown with yellow spots; arms brown with yellow flecks; pinnules brown or black with yellow spots; oral disk and ambulacra also brown with yellow spots. This crinoid occurs in shallow zones (2–5 m) in areas exposed to strong current or wave activity (Table 3).

LIFE HABITS: *Comanthus samoanus* is typically found nestled within the branches of clumps of *Acropora* or other branching corals. Its short arms may be partially extended, and the pinnules are held in a multidirectional posture with only a slight angle between rows on the same side of the arm. The pinnules are curved toward the abambulacral side as in *C. parvicirrus*. Although this species is common in turbulent parts of the reef, a filtration fan is not formed. Rather, by virtue of its small size, *C. samoanus* appears to be adapted to a sheltered existence within coral branches.

Comaster gracilis (Hartlaub)

Comaster gracilis has not been previously reported from the Palau Islands. Clark (1931) gives its range as "from the Maldive Islands eastward to New Britain, Fiji, and the Macclesfield Bank."

COLOR VARIETIES:

1. Centrodorsal and division series white; arms becoming golden brown or orange beyond beginning of free arm; pinnules banded yellow and dark brown, with yellow tips; appearing solid orange from a distance (Figs. 4g, h).

2. Entirely black.

OCCURRENCE: In Palau, this species is most common along vertical fore-reef escarpments, such as that at Bailechesengel Island and at Mutremdiu (Table 3). It is less common at sites inside the outer barrier and fringing reefs.

LIFE HABITS: *Comaster gracilis* resembles *Comanthus parvicirrus* very closely in its living habits. It is found by day extending the arms from a crevice or other protected place in which the disk is attached by means of some of the arms; cirri are totally lacking (Figs. 4g, 6h). *C. gracilis* is more delicate in structure than *Comanthus parvicirrus* and in this regard parallels *Nemaster discoidea* in the tropical western Atlantic (Meyer, 1973a). The arms of this species appear to be exposed about as much as those of the cooccurring *Comanthus parvicirrus*; and *C. gracilis* also occurs within the coral framework where *C. parvicirrus* can also be found. It is not known whether *C. gracilis* emerges to any further extent by night.

Like other comasterid species living within the infrasturcuture of the reef, *C. gracilis* holds the arms and pinnules in a multidirectional array, but displays some unique features. First, the angle of offset between pinnules along one side of the arm can approach 90 degrees. Second, the offset of pinnules along one side of the arm shows a variable pattern. One pinnule deflected toward the ambulacral side is sometimes followed by two pinnules deflected toward the abambulacral side, then one deflected toward the ambulacral side and so on (Fig. 4h). In another pattern, the pinnules along one side of the arm are offset to form three rows instead of two. One pinnule is deflected toward the abambulacral side, the next is parallel to the plane of the ambulacrum, and the third is deflected toward the ambulacral side. The pattern is then repeated. Curvature of the pinnules appears to be lacking in this species.

Comaster multifidus (J. Müller)

Although known from the Philippines (Clark, 1931, p. 424), *Comaster multifidus* has never before been reported from the Palau Islands or Guam. Specimens collected from Palau are in agreement with the description given by Clark (1931). This species occurred at most stations investigated in Palau, but it is not one of the most abundant crinoids there. It was most frequently found at sites within the barrier and fringing reefs where some current flow prevails (Table 3).

COLOR VARIETIES:

1. arms bright orange, bright yellow in distal parts; pinnules dark (black or purple) or yellow where arm is yellow; may be entirely yellow.
2. arms and pinnules black or dark red.
3. arms green; some yellow distally.

LIFE HABITS: *Comaster multifidus* is practically cryptic by day, nestled within clumps of branching coral such as *Porites* or tucked into narrow recesses, so that only

a few arms are visible. This crinoid usually appears as a dense tangle of delicate arms. Based on a few observations made in Malakal Harbor, it is likely that this species emerges by night to a more exposed position. The pinnules are held with a slight offset and show abambulacral curvature.

Comatella maculata (P. H. Carpenter)

Comatella maculata has been previously reported from the Caroline Islands (Truk, Mortlock) by Hartlaub in 1891 (cited in Clark, 1931, p. 117).

COLOR VARIETY: All individuals of this species are solid dark red in color, including the oral disk, although the cirri may be somewhat lighter.

OCCURRENCE: Because it is entirely cryptic by day, *C. maculata* may have been overlooked at some localities (Table 3). It was particularly abundant in branching coral rubble along the edges of Ulong Pass.

LIFE HABITS: *Comatella maculata* is apparently a member of the nocturnal crinoid fauna in Palau. Although none were observed during night diving observations at Malakal Island, this species was found completely concealed by day at other localities in the Palau Islands. It is typically found curled up beneath coral heads or within thickets of dead *Acropora* branches. When disturbed, *C. maculata* crawls very rapidly back into shelter, with an almost fluid crawling motion.

Comatella nigra (P. H. Carpenter)

Comatella nigra is uncommon in the Palau Islands. This is the first record from the Palau Islands; its range was listed by Clark (1931, p. 97) as: "from Torres Strait, Northeastern Australia, and the Abrolhos Islands, Western Australia, northward to the Philippines and westward to Sumatra." It has been found at only two sites in Palau (Table 3).

COLOR VARIETIES:

1. arms orange; pinnules with white tips; basal color of pinnules uncertain (cf. *C. schlegeli,* variety 2).
2. arms dark brown to black proximally, brown distally; pinnules banded brown and black.

LIFE HABITS: Like *Comanthus parvicirrus, Comatella nigra* conceals the disk within recesses in the reef and extends the arms. One of the few available photographs of this uncommon species shows the arms extending outward and downward from an attachment point underneath the lower edge of the "skirt" of a massive coral head. The pinnules show a multidirectional posture.

Dichrometra flagellata (J. Müller)

Dichrometra flagellata was first reported from the Palau Islands by Hartlaub (1891, cited in Clark, 1941, p. 554). Specimens collected during the present study conform well to the description given by Clark (1941).

COLOR VARIETIES: The cirri are white or have the lateral and abambulacral sides darker. The division series and proximal parts of the arms are white, grey, or pink, with dark (red or purple) brachial articulations (Figs. 5a, b). The distal parts of the arms are banded with dark red, purple, pink, or white, or they can be solid brown or banded with brown and white. The pinnules can be white, yellow, brown, banded brown and white, red, or banded red and white, depending on the arm color. Individuals having a solid dark purple coloration have also been found.

OCCURRENCE: Because this species is highly cryptic during the day, the limited occurrence indicated in Table 3 is probably not a reflection of its actual distribution in the area studied. On the shallow reef of PMRI (Palau Marine Research Institute) at Malakal Island where nocturnal observations were made, *D. flagellata* was not very common. Of the five nocturnal species found there, *D. flagellata* ranks about fourth in abundance.

LIFE HABITS: This species appears to be very similar in its mode of life to *Lamprometra palmata*. Individuals have been found during the day, curled up beneath corals or within small caves in massive coral formations. At Malakal Island it was found that this species emerges by night and assumes a prominent position on top of coral heads where it forms an arcuate filtration fan (Fig. 5a). The food grooves are oriented downcurrent; the pinnules are planar and slightly curved. This species occurred only as single individuals within the same area inhabited by *Lamprometra* at Malakal Island, and was less abundant than *Lamprometra*. Its time of emergence is similar to that of the other nocturnal species and presumably so is its time of retreat at dawn. *D. flagellata* was also emergent during the day at the inner end of the tunnel leading to a marine lake (locality 13). Here a large individual was found crawling up onto a coral formation when the incoming tide began to flow through the tunnel.

Lamprometra palmata (J. Müller)

Lamprometra palmata was reported from Mortlock Island in the Carolines by Hartlaub (1891, cited in Clark, 1941, p. 506), but this is the first report from the Palau Islands.

COLOR VARIETIES: Most individuals have a distinctive green and white coloration which is highly variable in pattern. The arms usually have alternate green and white bands of variable length (Fig. 5c). The pinnules are white along white arm sections but can be green or green and white banded where the arms are green. Color patterns are similar from arm to arm, so that when the crinoid forms a filtration fan, a coordinated, concentric color pattern is displayed. Sometimes dark green bands

occur along the midsection of the arms, appearing almost black, or they can form a series of V's through extension of the dark pigmentation onto the adjacent pinnules (Fig. 7a). Other color forms are banded with brown or orange and white, sometimes mixed with green bands (Fig. 5d). Frequently the division series are white with dark (green or brown) blotches marking the ends of the articular ridges of the brachials, imparting a zipper-like appearance to that part of the arm.

OCCURRENCE: Although *L. palmata* emerges only by night, it was found hidden within the reef infrastructure by day at most sites examined in the course of this study (Table 3). Nocturnal observations at Malakal Island suggest that this species is probably abundant in the area. At low tide, *L. palmata* was observed at about 30 cm depth in the intertidal notch of the northern tip of Ngeruktabel (locality 5). Elsewhere in the Pacific, this species has been observed on shallow reef flats (unpublished).

LIFE HABITS: *Lamprometra palmata* is one of the most conspicuous members of the nocturnal crinoid fauna in Palau. During the day this species remains curled up, completely hidden, beneath coral heads or deep within crevices or recesses. Within an hour before dusk, these crinoids begin to emerge from their hiding places. Within about 15 minutes, they crawl to the top of a coral head (*Porites lutea* at Malakal Island) and form an arcuate filtration fan normal to the direction of tidal current flow (Figs. 5c, d; Faulkner, 1974, Fig. 47, misidentified as *Comanthus parvicirra*). Arms on the downcurrent side of the fan are twisted to achieve the downcurrent orientation of all food grooves. The pinnules along each arm form a planar array which is slightly curved toward the abambulacral side. While a single individual usually occupies a coral head, some pairs have been seen as well as a few larger clusters. Retreat is practically complete by sunrise.

The only exception to the nocturnal emergence of *L. palmata* that was noted was within a dimly lit tunnel leading to a marine lake (locality 13). Here, during the day, a large number of this species was found fully expanded, forming filtration fans against the incoming tide. The greatly accentuated flow velocity through the tunnel deflected the filtration fans considerably although no retraction of the arms was observed.

At Malakal Island where the nocturnal crinoids were studied, *L. palmata* is most closely associated with *Capillaster multiradiatus*, but the two species clearly occupy different spatial niches. *L. palmata* is completely exposed on the top or sides of the corals, while *Capillaster* extends the arms from a hiding place beneath the coral or along its sides (Fig. 5c). Both species are frequently found occupying the same coral formation. The three other species comprising the nocturnal fauna at Malakal Island, *Dichrometra flagellata, Stephanometra oxyacantha,* and *S. echinus,* also form filtration fans from perches on top of the corals. They were never seen to be closely associated with *L. palmata* or with each other.

Stephanometra echinus (A. H. Clark)

Stephanometra echinus is reported here for the first time from the Caroline

Islands. The closest previous record was from the Philippines (Clark, 1941, p. 412). Two specimens were found in Palau, both from the same shallow reef off the PMRI at Malakal Island. One specimen was collected, and it conforms well with the description of this species given by Clark (1941, p. 410).

COLOR VARIETIES: Both specimens had distinct color patterns. The specimen collected had bright red-orange arms and pinnules, with some distal parts of the arms and their pinnules orange. Some arms had clusters of narrow white bands extending to the proximal parts of the pinnules. The oral pinnules were a brighter shade of red-orange than the arms. Color photographs of the second specimen recorded a different color pattern but similar morphology and behavior (Fig. 5e). The cirri were banded with brown and white. The division series and proximal parts of the arms were densely flecked with brown spots on a whitish background, while the distal parts of the arms gradually acquired a narrow brown banding. The oral disk and proximal pinnules were also brown spotted, but the pinnules became distinctly brown banded along the distal parts of the arms. At a distance the crinoid had an overall golden appearance, with some distal parts of the arms and their pinnules yellow.

LIFE HABITS: Although only two individuals of this species have been observed, both were emergent at night and both perched on top of coral formations. One individual simply extended the arms radially, resting on or close to the coral. The second individual displayed a feeding posture somewhat similar to that of *Pontiometra andersoni* in that arms on the upcurrent side were raised up perpendicular to the flow, while the other arms arched laterally and downward toward the coral (Fig. 7b). The arrangement of the pinnules is planar. Because *S. echinus* has fewer arms than *Pontiometra,* the parabolic fan is not as dense a filter as in the latter species. In *S. echinus,* gaps may be present between the distal parts of the arm although pinnules of some adjacent arms nearly touch. It is possible that the lateral disposition of the arms seen in the one individual was a response to a slack current condition. Emergence takes place before total darkness as in other nocturnal species observed in Palau.

Stephanometra indica (Smith)

At Rmegethu Island, within the main lagoon of the Palauan archipelago, an aggregation of several small *Stephanometra* was found which differs from the other two *Stephanometra* species encountered. As these crinoids were all small (maximum arm length about 80 mm), it is possible that they are juveniles. Most have only P_2 elongated and spikelike, although in one specimen some P_3 are somewhat enlarged and spikelike, approaching the characteristics of *S. spicata* (Clark, 1941, p. 425). *S. spicata* was reported from Palau by Clark (1941, p. 433). In having only P_2 spikelike, most of these specimens conform to *S. indica,* which has been reported from Mortlock Island in the Carolines, but not from Palau (Clark, 1941, p. 453). The cirri are distinctly different from those of the other two species of *Stephanometra* and resemble those of *S. indica* illustrated by Clark (1915, p. 287, Fig. 340).

COLOR VARIETIES: These crinoids showed considerable color variation within the one small aggregation and differ from *S. echinus* and *S. oxyacantha*. The arms and pinnules were banded with reddish brown or purple and yellow or white in a variegated pattern; some were a solid dark, reddish purple, and others were solid pink or lavender with a white section of arms and pinnules midway along the arms.

LIFE HABITS: Specimens of this species were found beneath slabs of coral rock. Thus it seems likely that this crinoid is nocturnal, but no further information is available.

Stephanometra oxyacantha (Hartlaub)

This species has been previously reported from as close as the Philippines (Clark, 1941, p. 423), but has never before been reported from Palau or the Caroline Islands. Specimens referred to this species possess spikelike oral pinnules through P_5 and conform to the description of *S. oxyacantha* given by Clark (1941, p. 419). It is clearly distinct from the other two species of *Stephanometra* found in the Palau Islands.

COLOR VARIETIES: Although *S. oxyacantha* is highly variable in coloration, the presence of black or brown brachial articulations is a consistent feature found in most individuals. In addition, this crinoid usually possesses brown and white banding of the cirri, arms, and pinnules, but the pattern varies considerably and the distal parts of the arms and their pinnules can be solid brown (Fig. 7c). In some individuals the arms appear orange or golden with some white arm bands and white pinnules.

OCCURRENCE: Table 3 indicates that this crinoid is widely distributed throughout the study area. It is usually found as single individuals, but aggregations of several individuals were seen at Malakal Island on the shallow reef off the PMRI.

LIFE HABITS: Although most individuals of *S. oxyacantha* are fully emergent at night, some individuals are day-active. During the day, this crinoid is frequently seen within the infrastructure of the reef, typically clinging to the underside of ledges or small recesses and forming a pendant arcuate fan (Fig. 7c). The pinnules are planar or slightly curved. Sometimes the arms are not aligned in a fan. This crinoid is something of an exception to the usual multidirectional pinnule posture for crinoids dwelling within the infrastructure. It would be interesting to know if this crinoid occupies plances where it is exposed to a persistent direction of current flow even though it lives well within the zone where reef topography breaks up uniform flow patterns.

Observations made at Malakal Island during night diving showed that *S. oxyacantha* emerges by night to occupy perches on top of coral heads where it forms a vertical filtration fan. One cluster of several individuals was observed on a single coral formation. By day, many of these crinoids could be located without overturning coral heads, but most had clearly retreated to the lower edges of the coral head. These limited observations suggest that other reefs where a few *S. oxyacantha* were seen by day may actually harbor more individuals which emerge only at night. A single

individual of this species was found fully expanded by day, attached to an alcyonacean, but at the inner entrance to a tunnel feeding a marine lake (locality 13). In this twilight situation, other normally nocturnal species were also active. It is possible that *S. oxyacantha* is intermediate in light sensitivity between strictly nocturnal and light tolerant species.

Cenometra bella (Hartlaub)

This is the first report of *C. bella* from the Caroline Islands. The closest previous record is from the Philippines (Clark, 1947, p. 40).

COLOR VARIETIES: Several distinct color varieties were observed in this species (Figs. 5f, g). The cirri range from brown through light to dark red, and usually contrast sharply with the arm coloration. The arms can be white, grey, or silver, and also yellow, golden, or orange, olive drab, brown, dark red, or even black. There are often small dark spots on the arms, especially in the proximal parts. The pinnules usually contrast in whole or in part with the arms, having the same range of colors as the arms. In a variant with silver-grey arms, newly formed arm groups were dark red, matching the cirri.

OCCURRENCE: Table 3 shows the *C. bella* was widely encountered throughout the area studied. Its distribution is correlated with that of its preferred substrata, wire corals such as *Junceella* and *Cirrhipathes* and gorgonacean fans. These coelenterates are found in the greatest concentrations along the current-swept passes between reefs and islands, and along the steep drop-offs of the outer reefs.

LIFE HABITS: *Cenometra bella* is invariably found clinging to antipatharian wires (*Cirrhipathes*), ellisellid gorgonaceans (*Junceella*), and various gorgonacean fans (*Subergorgia, Melithaea*) (Figs. 5f, 7d; Faulkner, 1974, Figs. 26, 51). In this way *C. bella* maintains an elevation of a meter or more above the subtratum and lives essentially as a functional stalked crinoid. While this species usually occurs as single individuals, clusters of two or more are found clinging to single "wires." In one instance, eight individuals were clinging to a single antipatharian, forming a tight, mop-like cluster (Fig. 7d).

Cenometra bella forms a radial filtration fan normal to the direction of current flow (Fig. 3b). The elongated second pinnules of each arm form a dense palisade covering the oral disk (Fig. 7e). Frequently, a parabolic fan is formed by the aboral curvature of the arms. This posture is very similar to that observed in the stalked isocrinids *Cenocrinus asterius* (L.) and *Endoxocrinus parrae* (Gervais) in the Caribbean (Macurda and Meyer, 1974). A common filtration fan may be formed by clusters of *Cenometra* on single "wires." A pair attached on opposite sides of a "wire" were observed with the expanded arms ovrlapping (Fig. 5f). This behavior, also observed in *Nemaster grandis* in the Caribbean (Meyer, 1973a), may facilitate the baffling of water flow through the feeding fan which could enhance the capture of

food particles. During conditions of little or no current, *C. bella* will hold the arms incurved toward the oral disk, or curved in the opposite manner, with the planar arrays of pinnules oriented in different directions.

Cenometra bella is capable of active swimming but may only occasionally utilize this mobility. On two occasions in Palau, we observed single individuals swimming freely about 1–2 m off the bottom. These crinoids had not been disturbed by our activities. The graceful swimming motion lasted for about a minute at a time, after which the crinoid would hold the arms upward, fold the pinnules parallel to the arms, and drop rapidly to the bottom. After remaining stationary for a few minutes swimming was resumed. Although there were antipatharian "wires" in the immediate area, the crinoid did not come in contact with one while under observation. In one area in 1976 (locality 3) a total of 15 *C. bella* was counted on "wires" surrounding a large submerged rock at a depth of about 4–5 m. In 1977, 20 individuals were counted in the same area. Around an adjacent rock tags were attached in 1976. In 1977, one tagged "wire" was relocated with a pair of crinoids clinging to it which had also carried a pair of crinoids the year before. Another tagged "wire" with a single crinoid attached was also relocated as well as a tagged "wire" with no crinoid. These observations suggest that *C. bella* maintains a stable population in a favorable area and that individuals may remain in the same exact position for at least a year although they are capable of free mobility at any time.

Cyllometra manca (P. H. Carpenter)

A single specimen referable to this species was collected by W. B. Saunders from a *Nautilus* trap placed along the steep reef escarpment at Bailechesengel (locality 22) at a depth between 180 and 300 m. The specimen shows good agreement with the description given by Clark (1947, p. 137) and represents the first record of *C. manca* from the Palau Islands. The species was reported previously from as close as the Philippines (Clark, 1947, p. 167). A color photograph of the specimen taken before preservation was supplied by Saunders and shows the color in life to be banded with brown and white throughout the arms and pinnules. Specimens illustrated by Clark (1947, pls. 17, 20) also show a banded pattern on the arms and pinnules.

Oligometra serripinna (P. H. Carpenter)

Oligometra serripinna has not been previously reported from the Caroline Islands; the Philippines are the closest previous record (Clark, 1947, p. 227).

COLOR VARIETIES: The arms are light brown, orange, or have narrow brown and white bands. Solid variants have dark brown bands spaced widely or in clusters. The pinnules are brown or white or brown and white banded.

OCCURRENCE: *O. serripinna* is not at all common in the area surveyed in the Palau Islands. Although it requires gorgonacean fans as substrata, it is not as widespread

as the ecologically similar *Cenometra bella* (Table 3). *O. serripinna* has been observed in much greater abundance at Lizard Island on the Australian Great Barrier Reef.

LIFE HABITS: This small, ten-armed crinoid is found attached to gorgonacean fans and occasionally "wire" corals (Fig. 7f). The arms are held in a radial filtration fan. The pinnules show curvature toward the abambulacral side. Although it is found in large aggregations elsewhere in the tropical western Pacific, *O. serripinna* in Palau occurs in no more than twos or threes on single fans. In one instance, an individual of *O. serripinna* was found clinging to the elongated cirri of *Pontiometra andersoni.*

Pontiometra andersoni (P. H. Carpenter)

This large and conspicuous crinoid was first reported from Palau by Hartlaub (1891, cited in Clark, 1947, p. 16).

COLOR VARIETIES: The most common color form of *P. andersoni* is solid black, which upon closer examination sometimes is actually dark reddish brown or dark brown. One unusual variant had the following color pattern: cirri brown or yellow; division series and proximal parts of free arms dark brown, becoming light brown or golden distally; light and dark brown pinnules interspersed on some arms; newly formed arm and pinnule groups solid yellow (Fig. 5h). Another similar form had golden arms with dark brown pinnules, and another had brown arms and pinnules with the distal parts of the arms white, some pinnules white, and the cirri brown or white, some pinnules white, and the cirri brown or white or brown with the proximal parts white.

OCCURRENCE: Although widespread throughout the areas examined, *P. andersoni* was found in greatest abundance on the inner reefs of Palau, particularly along the passes (Table 3) at depths of 3–6 m. This crinoid occurs as single individuals on a single perch, in contrast to the aggregations seen in *Comanthus bennetti.* Its abundance in the passes is probably related to its rheophilic behavior.

LIFE HABITS: Like *Comanthus bennetti, Pontiometra andersoni* perches on top of prominent coral heads or rocks and is fully exposed to view; both species may be found in the same immediate area, sometimes occupying the same coral head, but not in close juxtaposition. The feeding posture of *P. andersoni* is entirely different from that of *C. bennetti.* By virtue of its extremely long cirri, *P. andersoni* appears to represent a secondary reversion to the stalked condition. These cirri do not so much wrap around objects as they act like stilts, raising the calyx a few cm above the substratum as would a short stalk (Fig. 5h).

P. andersoni forms a parabolic filtration fan from its elevated position (Fig. 5h). During periods of slack current, the crinoid holds the arms over the oral surface but then curving sharply aborally so that they are directed toward the substratum, giving the crinoid a "skirted" appearance (Fig. 3c). Occasionally individual arms will be held in different positions over the oral surface with the distal parts coiled orally.

When current begins to flow, the "skirt" of arms is tilted, becoming a parabolic filtration fan which is concave toward the source of the current (Figs. 3c, 5h). In some cases this can take place simply by the lifting of those arms on the upcurrent side. The downcurrent arms remain recurved aborally and virtually touch the substratum. Lateral arms are extended with the pinnules perpendicular to the flow with the food grooves downcurrent. The pinnules form a planar array along each arm or are slightly curved toward the abambulacral side. The arms frequently overlap, forming a multilayered filtration fan. The crinoid essentially forms a trap bounded above by the parabolic fan and below by the substratum. The parabolic fan maintains the downcurrent orientation of the food grooves on all arms, but without the twisting of the arms seen in species which form an arcuate fan. The feeding posture of *P. andersoni* bears a close resemblance to that of the stalked crinoids *Cenocrinus* and *Endoxocrinus* described by Macurda and Meyer (1974).

With increased current velocity, the upcurrent arms are raised up perpendicular to the current and are eventually splayed back in the adoral direction. Under extreme flow conditions, some arms are extended to the substratum to act as tethers by clinging with pinnular hooks as in *Comanthus bennetti.* We have not seen any individuals of this species dislodged by the current or even crawling into sheltered positions. *P. andersoni* is capable of swimming but we have not observed this occurring naturally.

Dorometra nana (Hartlaub)

The occurrence of *D. nana* in the Palau Islands is reported here for the first time. The closest previous record is from the Philippines, and the species has been recorded from the Marshall Islands to the east (Clark and Clark, 1967, p. 74).

COLOR VARIETIES: Although this species displays considerable color variation at other western Pacific localities, the Palauan population is generally solid dark red or reddish brown.

OCCURRENCE: Despite its cryptic living habits, *D. nana* was found at most of the sites where the crinoid fauna was represented by locally high species diversity (Table 3). It was found in the greatest abundance within branching coral rubble in Ulong Pass (locality 20), a channel through the western barrier reef which experiences high rates of tidal current flow. It is possible that the cryptic habits of this small crinoid require a strong current flow to provide adequate exchange of food-carrying waters through the reef infrastucture. Its distribution in the area studied is, however, very likely to be more widespread than indicated in Table 3.

LIFE HABITS: This small species has been found only beneath platy corals, within thickets of branching coral, or within heaps of coral rubble. Sometimes as many as 15–20 individuals were found together. When exposed by overturning the coral, the arms of *D. nana* are usually extended, while species like *Capillaster multiradiatus* and

Lamprometra palmata have the arms tightly coiled. It is possible that *D. nana* is entirely cryptic, existing in open spaces within the reef framework and capturing food particles carried through by the currents. Another possibility is that this species, like its Caribbean relative *Ctenantedon kinziei* Meyer, emerges by night. However, none were observed among the abundant nocturnal crinoids at Malakal Island. This is an actively swimming species but the swimming motion was observed only when it had been disturbed by our disruption of its living space.

Metacrinus nobilis (P. H. Carpenter)

A stalked crinoid was recovered from the outside of a shrimp trap hauled from a depth of about 360 m off Hospital Point, Guam, by R. Strong. The specimen (Fig. 8) is in good agreement with the description of *Metacrinus nobilis* given by Carpenter

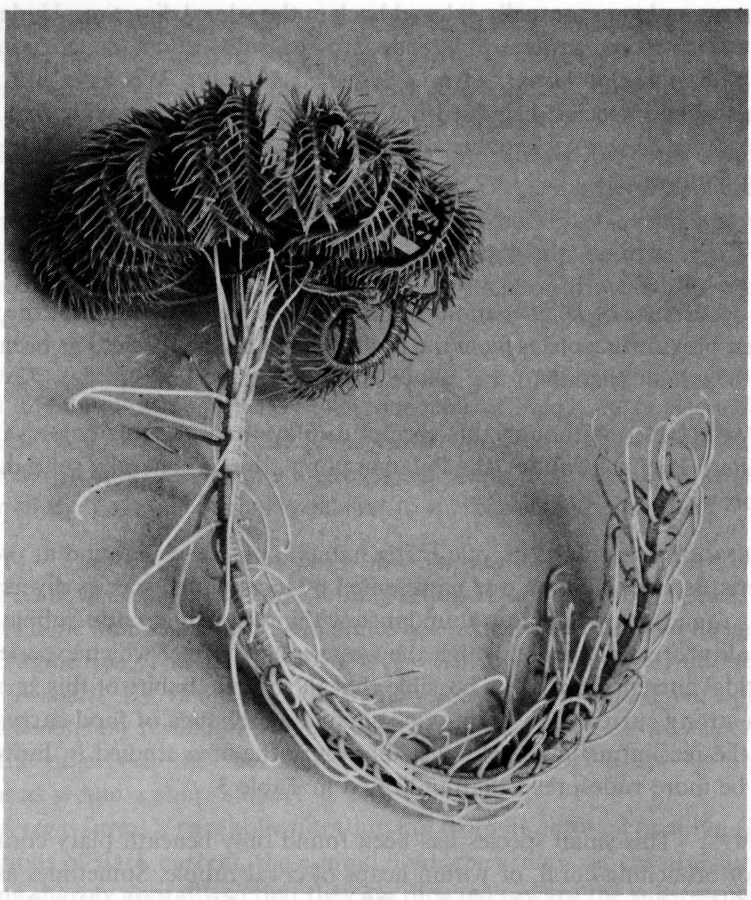

Fig. 8. *Metacrinus nobilis*, collected from 460 m off Hospital Point, Guam. (University of Guam Marine Laboratory photograph.)

(1884, p. 351, as *Pentacrinus nobilis*). The crown has 38 cm of stalk attached, with an abrupt termination at the distal end which appears to have been a fresh break, indicating a greater stalk length in life. The color in life was reported as tan to brown.

This is the first report of a stalked crinoid from Guam. *M. nobilis* was described originally from CHALLENGER Station 192 in the Kei Islands, from a depth of 256 m (Carpenter, 1884). The genus is known from Sumatra eastward to the Kermadec Islands, and from southern Japan to southeastern Australia (Clark, 1923). The specimen has been deposited in the collections of the Marine Laboratory, University of Guam.

Discussion

BIOGEOGRAPHIC IMPLICATIONS: Before this study was conducted, six species of crinoids had been reported from the Palau Islands (Table 1); the total now stands at 22, including one species from deeper waters. Previously, 12 species were known from Palau and the Caroline Islands together. Of the new records, nine species had been previously reported from as close as the Philippines, and one from no closer than New Britain and Fiji. Clark and Rowe (1971) listed 30 species from depths less than 20 m from the South Pacific Islands, which include Palau. Four species reported here (*Comantheria briareus, C.* sp. cf. *C. briareus, Comatella nigra,* and *Stephanometra echinus*) represent additions to the 30 species listed by Clark and Rowe.

The results of this study bring the Palauan crinoid fauna into much closer agreement with the total known from shallow waters of the South Pacific Islands as listed by Clark and Rowe. The Palauan crinoid fauna also is in agreement with the well known attenuation in species diversity away from the center of maximum diversity in the East Indian region. Clark and Rowe (1971) listed 82 species of shallow-water crinoids from this region, and 45 species from the Philippine Islands. To date, the maximum species diversity of shallow-water crinoids recorded from a single area is about 30 species, from Lizard Island, on the northern Great Barrier Reef of Australia (unpublished). Clark and Rowe listed 43 species from North Australia. Because the total number of species present in a local area will certainly be less than that recorded from the entire subprovince, the total of 21 shallow-water species from Palau (as compared to 30 for the South Pacific) is probably close to the total number actually occurring in the archipelago. In contrast, 26 species of asteroids are known from Palau (Marsh, 1977), but a total of 55 species is recorded from less than 20 m throughout the South Pacific Islands (Clark and Rowe, 1971). The absence of himerometrid comatulids in Palau is noteworthy in view of their diversity elsewhere in the Indo-West Pacific (cf. Clark and Rowe, 1971).

MICROGEOGRAPHIC DISTRIBUTION: Table 3 presents a list of crinoid species found at each site investigated in the Palau Islands. Figure 2 shows the location of these diving sites. The number of dives made at each site is variable, so that the species lists developed are not the results of equal searching efforts. For some sites, the actual number of species present may well exceed that indicated in Table 3. Nevertheless, we

are reasonably confident that our data reflect real differences that exist in crinoid diversity between sites. Notably, the most diverse site, at the western tip of Ngeruktabel, with 14 species, was visited only a few times, compared to many dives made at Mutremdiu. The sites having highest diversity of crinoids tend to be those lying within the fringing reef, as opposed to those located on seaward reefs. Sites along the eastern fringing reef (9, 10) showed markedly lower numbers of species than sites within passes through the reef (6) on this side. The outlying reef to the east, Uçhelbeluu (12), supports at least nine species, with some present in abundance. However, most of our efforts were concentrated along the protected western side of this reef.

Our work on the western barrier reef was limited to only a few sites. The exposed reef escarpment along the west side of the Ngemelis Islands (21) was remarkably poor in crinoids, but the same reef escarpment, where it turns inward to face southeast (22) was rich in crinoids. Likewise, Ulong Pass (20) supported a good diversity, although we did not dive on the seaward front of the barrier here.

In general, the richest populations we observed were located in tidal passes or at other sites where current flow was an obvious environmental feature. The richest site, a promontory near the western tip of Ngeruktabel (14), appeared to be exposed to a gentle current flow parallel to the western limb of the island. Much more severe current conditions were encountered in the narrow tidal passes (6, 7, 11, 20). It seems reasonable to suppose that local distribution and abundance of crinoids in the Palau Islands is controlled to a large extent by prevailing patterns and persistence of current flow. Conditions on exposed, seaward reefs may be too severe for large and diverse populations of crinoids to develop. The optimal conditions appear to be persistent current flow, probably at rates less than 1–2 knots, and protection from severe wave action. Tidal passes and the protected inner reefs provide these conditions in the Palau Islands. This interpretation is in accordance with observations made in the Caribbean (Meyer, 1973a) and elsewhere in the western Pacific (unpublished).

The cryptic behavior of many crinoid species and the widely spaced occurrence of other species make the estimation of crinoid population sizes extremely difficult. Birkeland et al. (1976) indicated the need for large sampling areas in order to obtain statistically significant samples of echinoderm population sizes along the fringing reef south of Malakal Island (Table 3, locality 2). In their survey, a maximum density of 1.75 crinoids per 100 m^2 was obtained from a daytime count of transects along the reef margin. The coral patch and sand zone of the same reef showed only 0.4 crinoids per 100 m^2 and the need for a nocturnal survey was indicated. During our study, considerable attention was focused on the population of nocturnal crinoids inhabiting the same fringing reef along Malakal Island, but at a site just off the Palau Marine Research Institute (locality 1), about 500 m north of the site surveyed by Birkeland et al. The nocturnal study was conducted within a patch reef 6–33 m offshore. During the day, virtually no crinoids could be seen exposed in this area. A nocturnal survey of this area, totaling 270 m^2, revealed a total of 139 crinoids belonging to four species, all emergent for nocturnal feeding. This yields an average density of 0.51 per 1 m^2. We found a total of 11 species at the site surveyed by

Birkeland et al. (locality 2), including the cryptics most common in our nocturnal survey. If the densities observed along the western fringing reef at Malakal Island hold for the nearby southern fringing reef, they would represent a 29-fold increase of the nocturnal crinoid population over the maximum visible by day in that area. Further results of the nocturnal survey will be reported in a separate publication.

LIFE HABITS OF PALAUAN CRINOIDS: This investigation has made possible the first comprehensive summary of the life habits of a diverse fauna of comatulid crinoids in the western Pacific. Table 4 summarizes available information on the life habits of the Palauan crinoids. This classification provides a first approximation to understanding the ecologic differentiation of these crinoids based on the following factors: 1) activity period, 2) feeding posture, and 3) living position. These factors may represent some of the major niche dimensions of these species, although it is clear that a great deal of overlap occurs between species within this classification.

ACTIVITY PERIOD: The majority of crinoid species found on Palauan reefs are active during daylight hours (Table 4). These species are generally wholly or partially visible without overturning or breaking open rocks and coral formations. We assume they are actively feeding because the tube feet are extended. In the Caribbean, *Nemaster rubiginosa* displays partial extension of the arms by day, but may rarely emerge completely at night (Meyer, 1973b). The extent to which partially emergent Palauan crinoids increase their emergence by night is not completely known. *Comaster multifidus* is visible by day, but is generally nestled within thickets of branching coral. By night this species can show complete emergence. Some individuals of *Stephanometra oxyacantha* form filtration fans in restricted spaces within the reef infrasturucture by day, while others are entirely concealed with the arms coiled. By night this species shows complete emergence and formation of a filtration fan on the tops of coral formations. Further nocturnal observations are needed to determine whether additional species follow similar patterns. No Palauan species are known to be day-active and nocturnally inactive.

Several species in Palau are practically never visible by day unless they are exposed by overturning or breaking into rocks and coral formations (Table 4). When found by day, these crinoids have the arms coiled and the pinnules folded along the arms; by night they are wholly or partially emergent. These species thus appear to possess a strictly nocturnal activity pattern. Table 3 shows that nocturnal species occur at the same sites with species presumably active around the clock. However, it is apparent from observations made on the shallow reef in Malakal Harbor that nocturnal species can also occur in abundance at sites where other day-active species are uncommon. The extent to which this occurs throughout the Palauan archipelago must await further observations.

The number of nocturnal crinoids reported here is the highest yet recorded. On Caribbean reefs, two strictly nocturnal species are known (Meyer, 1973a). Rutman and Fishelson (1969) and Fishelson (1974) reported three nocturnal species from Red Sea reefs, including *Capillaster multiradiatus* as reported here and a different species of *Lamprometra*.

Table 4. Life-habit classification of Palauan shallow-water crinoids.

I. Species with 24 hour activity pattern.
  A. Species forming a filtration fan.
    1. Occupy perches, fully exposed to view.
      a. *Comanthus bennetti*—arcuate fan.
      b. *Pontiometra andersoni*—multilayered parabolic fan.
      c. *Comantheria briareus*—multilayered arcuate or parabolic fan, not deeper than 12 m.
      d. *Comantheria* sp.—as in *C. briareus* but occurs below 15 m.
    2. Cling to octocorals.
      a. *Cenometra bella*—prefer ellisellid gorgonians; radial or parabolic fan.
      b. *Oligometra serripinna*—prefer octocoral fans; radial fan.
    3. Hang down beneath ledges, within small caves within reef infrastructure.
      a. *Stephanometra oxyacantha* (part)—arcuate fan.
  B. Species forming a multidirectional posture, dwelling within reef infrastructure with only arms exposed.
    1. Larger, more robust species.
      a. *Comanthus parvicirrus*—attaches with arms, lacks cirri.
      b. *Comanthina schlegeli*—lacks cirri; about 100 arms.
      c. *Comatella nigra*—possesses cirri.
    2. Smaller or more delicate species.
      a. *Comanthus samoanus*—small; attaches within clumps of branching coral.
      b. *Comaster multifidus*—concealed within thickets of branching coral; possible complete emergence by night.
      c. *Comaster gracilis*—long, slender arms.

II. Species active only at night.
  A. Species forming a filtration fan.
    1. Occupy perches, fully exposed to view.
      a. *Lamprometra palmata*—arcuate fan.
      b. *Dichrometra flagellata*—arcuate fan.
      c. *Stephanometra echinus*—parabolic fan.
      d. *Stephanometra oxyacantha* (part)—arcuate fan.
    2. Attach within infrastructure, extending only arms.
      a. *Capillaster multiradiatus*—arm fan.
  B. Presumably nocturnal but feeding position unknown.
      a. *Comatella maculata.*
      b. *Stephanometra indica.*
      c. *Dorometra nana*—possibly cryptic within infrastructure.

FEEDING POSTURE: Palauan crinoids can be broadly differentiated on the basis of five general feeding postures which were defined previously (Fig. 3; Table 4). Although each of these feeding postures is utilized by several species, it should be clear from the detailed analyses of living habits that practically every species possesses unique morphological or behavioral characteristics. These species-specific features differentiate most species that utilize a given general feeding posture. For example,

both *Cenometra bella* and *Oligometra serripinna* attach to octocorals and form a radial fan, but the surface area covered by the arm and pinnule arrays of *C. bella* is much greater than that of *O. serripinna* because *C. bella* is larger and has at least twice as many arms. *Comanthus parvicirrus* and *Comaster gracilis* both utilize a multidirectional posture from similar living sites within the reef infrastructure, but the two species differ in arrangement of the pinnules.

On the other hand, feeding postures of some species are closely similar, as in the arcuate fans seen in *Lamprometra palmata* and *Dichrometra flagellata*. The multidirectional postures assumed by *C. parvicirrus, Comanthina schlegeli,* and *Comatella nigra* are also quite similar. As yet, we have no indication as to the consequences of these feeding postures for resource utilization. Investigation of gut and feces contents is currently in progress.

LIVING POSITION: Four major categories of living position can be recognized among the Palauan crinoids: 1) occupation of exposed perches, 2) clinging to narrow objects such as octocorals, 3) hanging down beneath ledges or within smalll caves, and 4) attachment within the reef infrastructure. As observed in the Caribbean (Meyer, 1973a), a close correlation exists between living position and feeding posture. Species that occupy perches utilize arcuate or parabolic filtration fans to feed from unidirectional currents. Species clinging to octocorals also form a radial or parabolic fan for current-feeding. In contrast, species inhabiting the reef infrastructure practically all utilize a multidirectional posture. It has been suggested that the multidirectional posture is an adaptation to a multidirectional regime of water movement prevailing within the reef infrastructure (Meyer, 1973a). In Palau, two species inhabiting the infrasturcture form planar pinnule arrays and arm fan or a full filtration fan. One of these, *Stephanometra oxyacantha*, is not an obligate inhabitant of the infrastructure, because the majority of individuals emerge by night to occupy perches and form arcuate fans. However, those individuals visible during the day occur within the infrastructure where they are pendant from beneath ledges or within small caves (Fig. 7c), and form an arcuate fan. Possibly these day-active individuals prefer sites where flow is predominantly unidirectional, even though the site is well down within the reef framework. It is also possible that such species are incapable of offsetting the pinnules to form a multidirectional posture. *Capillaster multiradiatus* is the other possible exception to the observed correlation of multidirectional postures among inhabitants of the infrastructure. The arm fans formed by this crinoid are similar to those formed by *Comactinia echinoptera*, the principal nocturnal crinoid on Caribbean reefs (Meyer, 1973a, b). During nocturnal observations at Malakal Island, we observed that *C. multiradiatus* oriented the arm fans perpendicular to tidal current flow, despite the fact that the crinoids are extending the arms from crevices within the reef framework or from beneath corals. More detailed observations of the nature of flow through the infrastructure are needed, but it appears that *C. multiradiatus* responds to the principal unidirectional component of flow rather than intercepting all the lesser multidirectional components of flow in its microhabitat.

MORPHOLOGY OF THE TUBE FEET: In addition to the factors used to classify the life habits of Palauan crinoids in Table 4, the morphology of the tube feet may provide a further basis for differentiation. Meyer (1979) presented data on the length and spacing of the primary (particle-capturing) tube feet in nine Palauan crinoid species. Species forming filtration fans generally have shorter and more closely spaced tube feet than do species forming a multidirectional posture within the reef infrastructure. These relationships are in accordance with predictions of aerosol filtration theory applied to biological filters (Rubenstein and Koehl, 1977). A further consequence of this theory is that a filter having a particular morphology should fractionate a particular size range of particles for a given current velocity. If crinoid filters operate in the manner predicted, the species studied by Meyer (1979) should differentially fractionate a spectrum of particle sizes from the available range of particles. The statistical data reported by Meyer show considerable overlap between some species in length and spacing of the tube feet. However, other species are statistically different for these characters, suggesting that interspecific differences may exist in the size ranges of particles optimally filtered by distinct species. These intriguing possibilities are now being tested by examination of gut and fecal contents for some of these species. If theoretical predictions are borne out by these studies, morphological differentiation of the tube feet could dictate ecological differentiation between some of the Palauan species showing convergence in other aspects of their living habits as shown in Table 4.

ACKNOWLEDGMENTS

We gratefully acknowledge the support of our research through NSF Grant DEB 76–24334. We thank Dr. James P. McVey, former Director of the Micronesian Mariculture Demonstration Center, and his staff, especially MacDonald May, for providing facilities and assistance during our work in Palau. We thank Dr. Charles Birkeland and the staff of the University of Guam Marine Laboratory for hospitality and assistance during our visit to Guam and for the loan of crinoid specimens from Guam. Kaniaulono Meyer provided diving assistance in 1976. Gregory A. Minnery served ably as research assistant and diving partner to Meyer in 1977. We thank Belhaim Sakuma and the staff of Micronesian Divers for diving facilities and assistance during our work in Palau. We thank Dr. Bruce Saunders for providing the specimen of *Cyllometra manca*. The manuscript has been typed by Jean Carrol; and figures have been drafted by Nancy Alexander and James Williams. Permission for publication has been granted to Macurda by Exxon Production Research Company.

References Cited

Birkeland, C., R. T. Tsuda, R. H. Randall, S. S. Amesbury, and F. Cushing. 1976. Limited current and underwater biological surveys of a proposed sewer outfall site on Malakal Island, Palau. Univ. of Guam Mar. Lab., Tech. Report no. 25.

Breimer, A. 1969. A contribution to the paleoecology of Paleozoic stalked crinoids. Proc. Koninkl. Nederl. Akad. Wetensc. Amsterdam, series B. 72(2): 139–150.

Carpenter, P. H. 1884. Report on the Crinoidea collected during the voyage of H. M. S. "Challenger" during the years 1874–1876. The stalked crinoids. Report Sci. Results Voyage "Challenger," Zool. 11: 442 pp.

Clark, A. H. 1915–1950. A monograph of the existing crinoids. The comatulids. Bull. U. S. Natl. Museum 82. 1(1–4).

————. 1923. A revision of the Recent representatives of the crinoid family Pentacrinidae, with the diagnosis of two genera. J. Wash. Acad. Sci. 13: 8–12.

————. 1954. Records of Indo-Pacific echinoderms. Pac. Sci. 8: 243–263.

Clark, A. H., and A. M. Clark. 1967. A monograph of the existing crinoids. The comatulids. Bull. U. S. Natl. Museum 82. 1(5).

Clark, A. M., and F. W. E. Rowe. 1971. Monograph of shallow-water Indo-West Pacific echinoderms. British Museum (Nat. Hist.) Publ. no. 690, 238 p.

Clark, H. L. 1915. The comatulids of Torres Strait: with special reference to their habits and reactions. Pap. Dept. Mar. Biol. Carnegie Inst. Washington, D. C. 8: 97–125.

Faulkner, D. 1974. This Living Reef. Quadrangle/The New York Times Book Co., New York. 184 p.

Fishelson, L. 1974. Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. Mar. Biol. 26: 183–192.

Macurda, D. B., Jr., and D. L. Meyer. 1974. Feeding posture of modern stalked crinoids. Nature. 247: 394–396.

Magnus, D. B. E. 1963. Der Federstern *Heterometra savignyi* im Roten Meer. Nat. Mus. Frankfurt. 93(9): 355–368.

Marsh, L. M. 1977. Coral reef asteroids of Palau, Caroline Islands. Micronesica. 13(2): 251–281.

Meyer, D. L. 1973a. Feeding behavior and ecology of shallow-water unstalked crinoids (Echinodermata) in the Caribbean Sea. Mar. Biol. 22: 105–129.

————. 1973b. Distribution and living habits of comatulid crinoids near Discovery Bay, Jamaica. Bull. Mar. Sci. 23: 244–259.

————. 1976. The Crinoidea of the Rumphius Expedition II. Oseanologi di Indonesia, 1976, no. 6: 39–43.

————. 1979. Length and spacing of the tube feet in crinoids (Echinodermata) and their role in suspension feeding. Mar. Biol. 51(4): 361–369.

Meyer, D. L., and D. B. Macurda, Jr. 1977. Adaptive radiation of the comatulid crinoids. Paleobiol. 3: 74–82.

Meyer, D. L., C. G. Messing, and D. B. Macurda, Jr. 1978. Zoogeography of tropical western Atlantic Crinoidea (Echinodermata). Bull. Mar. Sci. 28(3): 412–441.

Rubenstein, D. J., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111: 981–994.

Rutman, J., and L. Fishelson. 1969. Food composition and feeding behavior of shallow-water crinoids at Eilat (Red Sea). Mar. Biol. 3(1): 46–57.