Brittlestar Color-Change and Phototaxis (*Echinodermata: Ophiuroidea: Ophiocomidae*).

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Abstract. In the first decisive study of color-change in brittlestars, four Caribbean species, *Ophiocoma echinata, O. paucigranulata, O. pumila,* and *O. wendti* are reported to change color from day to night. Color-change is most striking in *O. wendti,* which is dark brown during the day, and is banded gray and black from dusk to dawn. The transformation occurs over a 3 to 4 hour period and is effected by chromatorphores which appear to respond to illumination, independently of the central nervous system. Color-change may also be mediated by an endogenous rhythm. *Ophiocoma wendti* is more responsive to light than the other 3 species tested. It reacts to lower levels of illumination at night than during the day, exhibiting negative phototaxis in moonlight as well as in sunlight. I suggest that color-change may expose (or shield) photosensitive tissues that control the brittlestar's detection of shaded fissures in the reef. Thereby, chromatophore activity may be connected with the brittlestar's chief defense from predators, the ability to detect shadow and escape into darkened crevices. Although experiments to date with predacious fish are equivocal, the color patterns of *Ophiocoma* species may provide protective camouflage.

Problem

This paper is the first unequivocal report of color-change in brittlestars. It demonstrates that color, in members of the genus *Ophiocoma,* is produced by chromatocytes (cells with fixed pigment granules) and by chromatophores (cells with pigment granules that disperse in response to light). Color-change is particularly fascinating and enigmatic in these organisms lacking discrete photo-sensory organs, since it was long presumed that animals without eyes, such as the echinoderms, could not change color (Parker, 1931). Despite the belated recognition of color-change in the sea urchins (reviews in Yoshida, 1966; Millott, 1975; Weber, 1983), the idea persists that colors are fixed in brittle-stars and other echinoderms. Von Uexküll (1905) mentioned that a brittlestar, *Ophioglypha lacertosa* (= *Ophiura ophiura* Lamarck), turns a shade darker („wird plötzlich um eine Nuance dunkler") when disturbed by a shadow, but his assertion was dismissed (Mangold, 1909) and never retested. Until the present study, the colors of brittlestars were ascribed to pigment-cells of permanent shape; unreactive to changes in illumination (Fontaine, 1962 a, c).

The selective value of the color-patterns of brittlestars and many other organisms, has not been systematically assessed. An accepted explanation for the coloration of the drab majority of animals is that unpretentious colors and patterns render creatures inconspicuous to visual predators (Cott, 1940). Indeed, elegant experiments have proved that sober hues provide effective protection from predation (Endler, 1978, 1980). Some organisms that change color to match their background are also vivid evidence of the utility of pigmentation patterns. Without such examples, the invocation of "cryptic coloration" would seem to be a delusion of panglossian biologists!

The dull pigmentation patterns of brittlestars, perhaps uncritically, have been thought to provide protective coloration. Hyman (1955, p. 599) noted that "in general the coloration of ophiuroids is on the sober side . . . epizoic species may show adaptive coloration" (see Fontaine, 1962 b, for similar conclusions). Since brittlestars lack discrete photosensory organs (Pentreath & Cobb, 1982; Stubbs, 1982) their pigmentation certainly is not influenced by sexual selection favoring conspicuous colors.

With the recognition of color-change in brittlestars, adaptations besides crypsis may be considered to explain the significance of brittlestar pigmentation

and color patterns. In particular, this report links color-change with brittlestar escape behavior and nocturnal habits. I suggest that the function of color-change is not entirely to protect the animal from visual predators. Rather, chromatophore activity may regulate the exposure of brittlestar photosensitive tissues to light, facilitating negative phototaxis under a range of light intensities. Nocturnal activity, which is a brittlestar defense from diurnal predators (HEND-LER, 1984), involves negative phototaxis. Negative phototaxis is also the basis of another critical brittlestar defensive behavior: rapid retreat to dark, sheltering crevices.

Somewhat analogous conclusions have been reached in the literature on diadematoid sea urchins. Acting as independent effectors, sea urchin chromatophores respond to light (WEBER, 1983). As a result of chromatophore activity, some black portions of the sea urchin test turn gray at night. Thereby, the chromatophores purportedly adjust the sensitivity of subdermal photosensitive tissues which regulate the response directing the urchin's defensive spines towards shadows. The physiological basis of these spine movements (e. g., the photoreceptive systems and reflex responses) have been investigated at length. However, the ecological advantages of the echinoid shadow response are little understood (YOSHIDA, 1966; MILLOTT, 1975). The mechanisms of color-change and photosensitivity may be analogous in diadematoid sea urchins and ophiocomid brittlestars, but they seem to control a possible "fight" reaction of the sea urchin's spines and the "flight" response in brittlestars.

· The organisms I studied include all the Caribbean species of the genus *Ophiocoma: O. echinata* (LAMARCK), *O. paucigranulata* DEVANEY, *O. pumila* LÜTKEN and *O. wendti* MÜLLER & TROSCHEL (the latter species often referred to as *O. riisei* LÜTKEN, prior to DEVANEY's (1970) contribution on the *Ophiocominae*). All four of these species were found to change color in a natural diel (day-night) light regime (Fig. 1). Like the other 15 species of this genus, they are common and widespread tropical littoral brittlestars and are certainly a prominent component of shallow-water coral reefs. Thus, brittlestar color-change may be readily observed *in situ*, and experimental material abounds for any physiologists or ecologists choosing to study the phenomenon.

Material and Methods

1. Study sites

Initially, I made observations on brittlestar color-change and diel (day-night) activity patterns in Panama (Galeta and Naos Marine Laboratories and San Blas Islands), from 1975 to 1978. However, this report is based primarily on research carried out during March/April and November/December 1983, on Carrie Bow Cay, from the Reef Crest to the Forereef Slope zones of the Belize Barrier Reef (for charts and habitat description see RÜTZLER & MACINTYRE, 1982).

The description of a diel activity cycle of Caribbean *Ophiocoma* species is based on a survey of a 290 m² quadrat at Galeta, Panama. The quadrat bridged the Back Reef from the shallow subtidal coralline zone, across an algal turf zone, to an artificial lagoon (HENDLER, 1977). The quadrat was censused at intervals through the day and night on 4–12 February, 15–20 October, and 5–15 November, during 1975. In all, 198 surveys of the area were made to count the number of *O. echinata*, *O. wendti*, and *O. pumila* arms extended from the reef and the number of brittlestars that had emerged from reef crevices.

A

B

E

F

Fig. 1. A comparison of day and night color-phases of four Caribbean *Ophiocoma* species. The identical individual of each species is shown at 1400 hours (day) and rephotographed at 2000 hrs (night). *Ophiocoma wendti,* disc diameter 18.8 mm: A, day; B, night.

C

D

G

H

Ophiocoma paucigranulata, dd 16.9 mm: C, day; D, night. *Ophiocoma echinata,* dd 16.6 mm: E, day; F, night. *Ophiocoma pumila,* dd 12.2 mm: G, day; H, night.

2. Handling and photography of brittlestars

The experimental animals were tested on the day they were captured. Specimens were retained in holding cages which were suspended in shallow water beneath the lab dock. The white plastic walls of the cages transmitted the diel light regime, and seawater circulated freely around the animals.

Unless otherwise noted, specimens were relaxed about 15 min before photography, by gradually adding magnesium sulfate crystals to the seawater in which the brittlestars were held. When returned to normal seawater, relaxed specimens revived completely after about 15 min. Brittlestars were photographed in a glass-bottomed aquarium over black velvet, and only photographs taken with identical exposures and strobe placement were analysed.

3. General color-change observations

To document diel color-change, five specimens each of *O. wendti, O. echinata, O. paucigranulata,* and *O. pumila* were photographed at 1400 hrs, returned to holding cages, and rephotographed at 2200 hrs. Individual's day and night photographs were compared.

These observations on color change employed 4 species, but only *O. wendti* was used for the experimental work described below.

This species was selected because its color-change was especially clearcut. *Ophiocoma wendti* varied from an almost uniform dark brown during the day (referred to as the 'homogeneous color-phase') to a grey and black banded pattern (referred to as the 'banded color-phase') at night.

The color patterns of individual *O. wendti* were examined for persistence from day to day. Five specimens were photographed at 2000 hrs on 31 March, then rephotographed at 2100 hrs, 1 April, and at 2200 hrs on 2 April. In order to ascertain the permanence of individual color marks, three black pigment bands nearest the disc on each arm (15 bands per animal) were compared in photographs for three consecutive nights.

4. Diel periodicity of color-change

To monitor the diel periodicity of color-change, 10 specimens of *O. wendti* in holding cages were observed at intervals between 1200 hrs on 30 March, through 1930 hrs on 3 April. At each examination, a count was made of the number of specimens with any banded arms. Banding was not always discernable on all 5 arms of a specimen at the same time, therefore, the total number of banded arms was also tallied. For the first 30 hours the brittlestars were examined at least every 3 hours (and even more frequently around dawn and dusk), thereafter observations were more sporadic.

Observations were made on severed arms of *O. wendti,* and on specimens without broken arms, to find out if isolated arms would maintain the same schedule of color-change as intact brittlestars. A single arm, broken near the disc, was taken from each of ten specimens of *O. wendti.* Each arm was placed in a small plastic box with a plastic mesh cover and the boxes were suspended alongside the holding cages and examined at the same times detailed in the preceding paragraph.

Six specimens of *O. wendti* from holding cages were photographed at 1600, 1700, 1830, and 2030 hrs to precisely determine the duration of the transition from the homogeneous to the banded color-phase under natural conditions. To examine the transitional color patterns the appropriate photographic images were projected side by side.

Portions of dorsal arm plates (hereafter abbreviated "DAP") chipped from *O. wendti* arms were examined to find whether the chips change color at the same time as whole brittlestars and severed arms. The lightly and heavily pigmented bands on the arm, which transform to gray and black bands in the nighttime color-phase, were distinguished with a dissecting microscope for experiments initiated during the day. In each experiment, "dark" and "light" DAP chips were dissected from each specimen with a razor blade and placed in filtered seawater. The chips were held in the laboratory in subdued light during the day and in darkness at night.

Three experiments were performed using DAP chips. A series of excised DAP chips from banded (nighttime) color-phase specimens (one dark and one light chip from each of 5 specimens) was prepared at 2330 hrs and examined after 8.5 and 19.5 hours. Another experiment was begun at 1900 hrs with two light and two dark DAP chips from each of five banded (nighttime) color-phase brittlestars. The chips were examined after 2 hours and 19.5 hours. A comparable experiment, but using homogeneous (daytime) color-phase animals, was started at 1240 hrs and the excised DAP chips were examined after 7 hours, 20 hours, and 30 hours.

5. Color-change in response to experimental illumination

Ophiocoma wendti kept in artificially darkened and lighted containers were compared to control animals kept in holding cages to test whether specimens would change color in response to an altered light regime. The artificial light and dark regimes were maintained in a darkened room. Experimental animals were held in 5-gallon, white plastic buckets containing aerated seawater. Continuous light was maintained under a row of incandescent bulbs (60 W, 120 V, Sylvania TWA 19-SM-B) mounted 0.61 m from the bottom of the buckets holding experimental specimens. Continuous dark conditions were created by covering another series of buckets with 4 layers of black plastic bags. During the experiment, the water temperature in the buckets varied between 26.5 and 27.0 °C.

An experiment was started at 2130 hrs with 10 *O. wendti* in the banded color-phase, and all were photographed. After 4 hours, 5 specimens held in the light and 5 specimens held in the dark were rephotographed and preserved. At 1200 hrs the following day another series of 10 *O. wendti* in the homogeneous color-phase, and an additional control series of 5 *O. wendti* from a holding cage, were photographed. After 4 hours, the 5 specimens held in the light, 5 specimens held in the dark, and the controls were rephotographed and preserved.

An experiment also was carried out to test the influence of artificial lighting conditions of shorter duration. Initially a group of *O. wendti* in the banded color-phase was photographed at 2130 hrs. After holding these specimens under fluorescent ceiling lights for 1.5 hours they were rephotographed. The following day, the same animals in the homogeneous color-phase were photographed at 0830 hrs, and rephotographed again one hour later after holding them in the dark. In this brief experiment, brittlestars were not relaxed before photography and were photographed in groups rather than individually.

The possibility of an endogenous color-change cycle in *O. wendti* was also tested. Twenty experimental and 5 control animals were maintained under the same conditions employed for the experiments above, of 4 hours duration. Ten *O. wendti* were held under incandescent lights, another 10 were held in the dark, and control specimens were kept in holding cages suspended from the laboratory dock. The experiment began at 1600 hrs, and all brittlestars were in the homogeneous color-phase. After 20 hours (at 1200 hrs) five animals were removed from each treatment and photographed, and after 30 hours (at 2200 hrs) the other five animals from each treatment were photographed. The control specimens were observed after 20 hours and photographed after 30 hours.

6. Color-change index and color names

The names used to describe brittlestar colors throughout this report are designated in the Inter-Society Color Council – National Bureau of Standards color charts (supplement to NBS Circular 553). In the experiments described in the sections above, color-change was assessed by assigning each arm of *O. wendti* in a photograph a banding index (hereafter abbreviated "BI") value ranging from 1 to 5. A BI of 1 indicates the arm is too deeply pigmented to distinguish a banded pattern. A value of 5 indicates that there are sharply contrasting black and gray bands on the arm. The values 2, 3, and 4 denote intermediate degrees of banding. A value of 2 indicates that bands are just barely perceptible; 3 that bands are shades of brownish-gray, and 4 that bands are shades of grayish-brown. For each treatment, the BI was determined for the 5 arms of each specimen and the indices of all arms were averaged to calculate a mean BI.

7. Preference for background color

To test the influence of background coloration on brittlestar movement, half of a transparent plexiglass seawater tray (45 × 30 × 10 cm) was rested on a piece of black plastic and the other half on a piece of white paper. The tray was uniformly illuminated by sunlight. *Ophiocoma wendti* were placed with their discs at the center of the tray. When a brittlestar remained in one location (generally a corner of the tray) for at least 5 min the location (black or white side) was recorded. If the brittlestar did not settle within 10 min, another experiment was initiated using a fresh specimen.

8. Reaction to shadow

The response of *O. wendti* to light and shadow was tested under two lighting conditions. Specimens were introduced to a white plastic tray (66 × 56 × 8 cm) holding 3 cm of seawater. One-third of the

tray was exposed to light, the middle ⅓ was covered by a black plastic sheet, and the remaining ⅓ of the tray was in the deep shadow of a wooden board.

One by one, specimens of *O. wendti* were placed in the tray with half of the disc at the edge of the shadow of the plastic and the other half in the light. The direction and speed of each animal was observed and the movement of the whole animal into shadow or light was timed with a stopwatch before the brittlestar was removed. Fifteen *O. wendti* were tested in the tray at 1000 hrs, under strong sunlight. The same specimens were tested again at 2100 hrs that night, with the tray dimly illuminated by a half moon behind clouds.

9. Sensitivity to illumination

The response of *O. wendti* to a graded series of illumination levels was tested to see whether the brittlestar's sensitivity to light was different during day and night. In day trials and night trials, 60 W light bulbs (described above) provided background illumination. The brittlestars were held in white buckets for the tests and allowed to adapt to the background illumination for one hour before assaying their reaction to a test light.

A microscope illuminator lamp (American Optical Company 11144 with GE 1493 bulb) was held against the side of the bucket to cast a 2.5 cm circle of light on the individual arm tips. An arm tip was exposed to the lowest illuminator setting for 15 sec. If the arm did not show a response by moving outside the circle of light, the illuminator was adjusted to the next setting. The increased light intensity was projected on the arm tip for 15 sec, and so on until the arm tip moved out of the light.

Experimental light intensities of the incandescent light source were measured with an underwater photographic exposure meter. The meter readings were converted to radiometric values (mw · cm^{-2} · nm^{-1}) by calibrating the meter against a 555 nm light source (the estimated midpoint of the meter's response curve). Values in mw · cm^{-2}, were calculated from the linear portion of the calibration curve, assuming that the meter's response covered a range from 400 to 700 nm. Because of the approximations used, the absolute values of irradiance used are not completely accurate, however, they do greatly help in estimating relative differences in light levels. The series of energy levels used were calculated as 1448.1 mw · cm^{-2} (at a 5 volt illuminator setting), 2082.0 (6 V), 2838.3 (6.5 V), 4185.0 (7.5 V). The threshold of sensitivity was considered to be > 4185.0 mw · cm^{-2} for arms that did not respond at the highest illuminator setting (7.5 V).

The same group of brittlestars was tested at 2312 hrs, in their banded color-phase and at 1330 hrs, in their solid homogeneous color-phase. The responses of 30 arm tips were recorded during each trial, and since 5 animals (for a total of 25 arms) were used for each trial, some arm tips were stimulated more than once.

10. Predation on *Ophiocoma* species

Observations were made to evaluate the reactions of predatory fishes to the 4 *Ophiocoma* species. The mean (and range) of disc diameters in mm, of the brittlestars used were as follows: *O. pumila*, 9.8 (8.1–12.8); *O. wendti*, 12.2 (9.2–15.6); *O. echinata*, 12.2 (10.4–17.7); and *O. paucigranulata*, 13.1 (10.9–16.2). Of course, the overall size of each of the species is a function of complex differences in arm dimensions which may not be accurately reflected by disc diameter measurements. Plastic bags containing 4 pre-measured specimens (one of each species) were opened at different locations on the Back Reef between 1400 and 1600 hrs. The number of fish attacks in 3 min was tallied for each set of specimens. The uniformly flat, sandy Back Reef terrain minimized the escape of brittlestars.

Another experiment was performed to determine whether predatory fish are equally capable of detecting and attacking *O. wendti* that are in homogeneous (daytime) or banded (night) color-phases. Specimens of *O. wendti* in the banded phase and the homogeneous phase were cooled in an ice-box. Within 12 hours, the specimens died but retained the same color-pattern they had when alive. Between 1600 and 1700 hrs, 6 pairs of solid and banded specimens were set out, about 10 m apart, on the Back Reef (in the same area as above). The number of attacks on each pair of brittlestars was tallied for three minutes. At the beginning of each experiment a living specimen of *O. wendti* was injured to attract fish to the area, and resealed in a plastic bag.

Results

1. Field observations on behavior

All four species of Caribbean *Ophiocoma* remain hidden during the daytime, and whenever their refuges are disturbed they rapidly retreat to protected crevices in the reef. Significant numbers of brittlestars begin to extend the tips of their arms from daytime shelters by 1600 hrs, with a profusion of arm tips visible by 1800 hrs. The arm tips are withdrawn between 0600 and 0800 in the morning. The pattern of activity of arms, similar to that observed in Belize, is evident in the census carried out on the Reef Flat at Galeta, Panama (Fig. 2).

On the Belize Barrier Reef, each species seems to occupy a preferred microhabitat, although all four species are sometimes collected under the same piece of coral rubble. The arms of *O. pumila* rest on the substratum or are raised in the water, extending from the sand at the base of massive coral heads and from very small holes and crevices in coral rubble. The arm tips of *O. echinata* protrude into the water or rest on calcareous algae and coral rubble. *Ophiocoma*
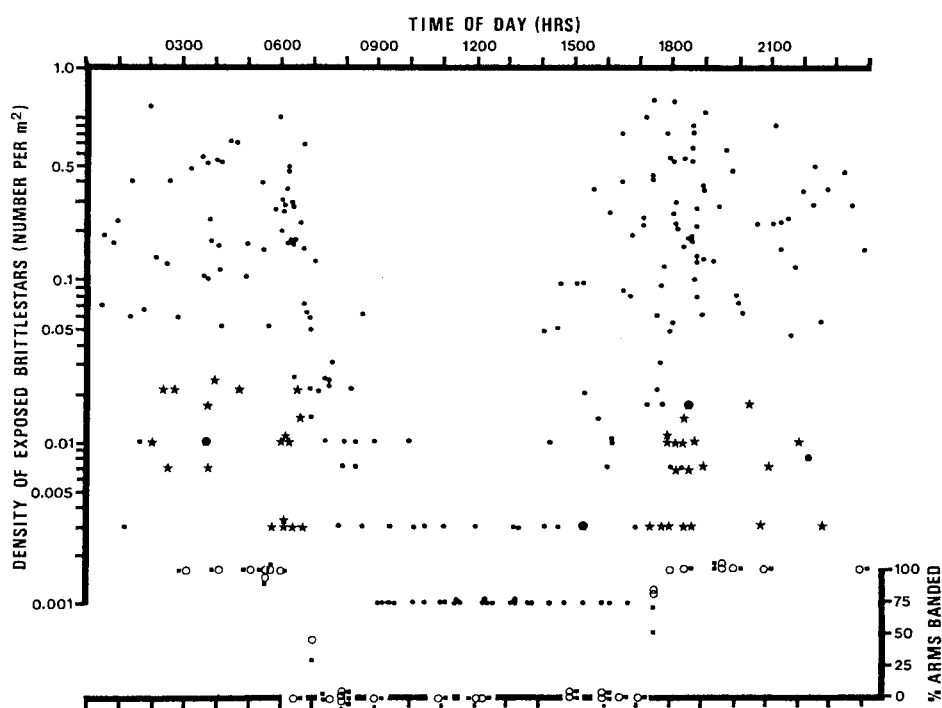

Fig. 2. A graph showing diel patterns of activity and color-change in *Ophiocoma* species. The density of arms protruding from the substratum (solid circles), and the density of brittlestars with the entire disc exposed (stars) for 198 surveys of a 290 m² quadrat illustrate day-night activity. Counts are combined for three species of *Ophiocoma*: *O. echinata, O. pumila,* and *O. wendti,* observed at Galeta Reef, Panama. The percentage of ten whole *O. wendti* with banded arms (open circles), and the percentage of ten severed arms (solid squares) showing a banded color-pattern are graphed to indicate the duration of the homogeneous and banded color-phases. The dusk and dawn transition between color-phases is evident for whole specimens and isolated arms from these data collected over four days at Carrie Bow Cay, Belize.

paucigranulata and *O. wendti* usually occupy larger, "fist-sized" cavities in the reef, between pieces of rubble or plates of coral such as *Agaricia tenuifolia* DANA. In many cases, specimens of *O. paucigranulata* and *O. wendti* inhabit the same crevice, with the arms of both species almost touching. The arms of *O. paucigranulata* are usually raised off the substratum with the distal 1 cm of the arm curled upwards. *Ophiocoma wendti* arms generally rest on the bottom, but occasionally ascend to catch floating particles or to browse on algal epiphytes.

At night, the four species are not equally sensitive to the narrow beam of light from underwater dive lights. *Ophiocoma pumila* shows little reaction to illumination from dive lights. The other species withdraw their arms into a crevice in response to light. *Ophiocoma paucigranulata* seems more sensitive to light than *O. echinata*, judging from its reaction speed. *Ophiocoma wendti* is obviously the most responsive species, rapidly reacting to small dive lights even when the light is attenuated with two layers of red cellophane. *Ophiocoma paucigranulata* and *O. echinata* do not react to dim red light.

2. Description of color-change in *Ophiocoma* species

Individuals of all four Caribbean *Ophiocoma* species change color in late afternoon. Although the color pattern of each specimen is unique, an overall shift of color from day to night can be delineated for each species. In general, the day to night change involves a replacement of brown shades by grays and black. The following descriptions are based on a comparison of photographs including those in Fig. 1.

The color-change of *Ophiocoma wendti* is particularly striking. During the day, specimens are brownish-black (the homogeneous color-phase), but some purely black pigmentation is evident on close inspection. The spines are brownish-gray, sometimes with brownish-orange tips. At night, the disc turns a grayish-brown and black, and the dorsal side of the arm develops striking gray (to white) and black bands. Two fine bands which ornament the paler colored DAPs and lateral arm plates are more evident at night than during the day. The ventral side of the arm remains unbanded. At night the arm spines often turn white basally, gray along the shaft, and medium-orange at the tip. The tube feet, colored by reddish chromatocytes, do not seem to change color from day to night.

Ophiocoma paucigranulata undergoes a relatively simple color-change. During the daytime, specimens are brownish-black with some black markings on the disc and a thin, light-brown stripe along the dorsal surface of the arm. At night, the overall color fades to dark gray, and the thin arm-stripe turns light gray or white.

In *Ophiocoma echinata*, regions that are brown during the day turn a gray color at night. *O. echinata* is more variegated and mottled than the other species examined and, during the day, most specimens are banded and spotted with shades of black, brownish-black, light grayish-brown, and white. At night, the predominant body colors fade to brown, black, white, gray, and grayish-brown, and the arm spines turn from brownish-gray to grayish-brown.

Ophiocoma pumila undergoes a comparatively subtle color-change. During the daytime, the disc color of different specimens varies from yellowish-brown,

brown, grayish-brown to brownish-gray. The arms are irregularly banded with off-white and brown shades. At night, light brown discs become a darker brown and the darker brown discs turn gray or black. The dark proximal arm-bands become more gray; however, the distal portions of the arms are nearly the same day or night, with brown-black bands on a whitish background.

3. Pigmentation pattern

The color of *O. wendti* depends on the distribution of chromatocytes, the density of chromatophores, and the aggregation or disperion of pigments in chromatophores. The characteristic banded pattern on the arms of *O. wendti*, the fine bands on the dorsal and lateral arm plates, and the dark irregular pattern on the disc are due to variations in the density of chromatophores. The reddish coloration of the tube feet, spine tips, and some disc granules probably is attributable to chromatocytes. Specimens in alcohol retain the overall brown color pattern, but alcohol extracts their red pigmentation.

The chromatophores of living *O. wendti* are blackish-brown cells which are capable of producing arborescent processes. The most punctate, isolated chromatophores range from 14 to 43 µm in diameter (n = 18) in specimens preserved at night. During the day, *O. wendti* appears to be almost uniform brownish-black due to a dispersal of chromatophore pigment in arborescent cell processes, but subtle patterns of darker and lighter pigmentation are due to different concentrations of chromatophores. At night, the chromatophores withdraw many of their arborescent processes, concentrating pigment, and as a result they appear smaller. At that time, *O. wendti* arms are banded black and gray. The features of the animal with dense concentrations of chromatophores look black, and the gray regions have low concentrations of especially punctate chromatophores. Even at night, when the chromatophore pigments are aggregated, many of the chromatophores have arborescent extensions and appear to be interconnected when examined at low magnification.

Fractured DAPs were examined microscopically to determine chromatophore distribution. The skeletal stereom in the outer portion of the DAP is transparent and has a knobbed architecture, while the stereom deeper in the plate is relatively dense and opaque. In DAPs preserved at night, the chromatophores appear to take a punctate shape and are deeper in the plate than during the day. In addition, during the day chromatophore pigments cover the stereom knobs of the DAPs, but at night the pigment concentrates around the sides of the knobs, and the tops of the knobs are exposed. If the epidermis is scraped from the skeletal plates of a specimen preserved during the day a considerable amount of pigment is lost. At night, comparable scraping removes relatively little pigment, strengthening the finding that chromatophore pigments are in deeper tissues than during the day.

4. Permanence of the overall pigmentation pattern

The dark arm bands of *O. wendti* do not shift position between day and night or from one day to the next. Fifteen bands examined for each specimen were in the

same position on 3 consecutive nights. Additional observations showed no change in the pigmentation pattern of the disc or the distal portion of the arms, although the colors composing the patterns altered between day and night. Moreover, the pigmentation patterns (areas of light and dark colors) of the other *Ophiocoma* species appeared the same at night and during the day. That is, the unique mottled or banded patterns of individual *O. echinata*, *O. pumila*, and *O. paucigranulata* are as permanent as the banded patterns of *O. wendti*.

5. Diel periodicity of color-change for whole specimens, arms, and arm plates of *Ophiocoma wendti*

Ophiocoma wendti shows a transitional color pattern as it changes from the homogeneous brown-hued daytime coloration to the gray and black, banded nighttime color-phase. The discs of transitional specimens (at dusk) are a mixture of black and dark grayish-brown or brownish-gray. At dusk, the arms are banded dark grayish-brown and black proximally, and with various shades of gray banding near the tips.

During the four days that *O. wendti* was monitored in holding cages, banded arms were first observed at 1700 hrs, and all arms were banded by 1800 hrs. The brittlestars remained banded during the night. The earliest that homogeneously dark arms were observed was at 0530 hrs (on one occasion) but a marked transition to the homogeneous color-phase occurred between 0630 and 0700 hrs. By 0730 hrs all animals displayed the homogeneous color-phase (Fig. 2).

The duration of the transition from the homogeneous to the banded color-phase was estimated by examining a series of color slides of 6 specimens taken at 1630, 1730, 1840 and 2025 hrs. The mean BI values of the 30 arms observed at each interval were respectively, 2.13, 2.97, 3.97, and 4.17. Since the BI value at 1630 hrs exceeded a normal daytime value, color-change must begin before 1630 hrs. The BI at 2025 hrs equalled the values found later in the night in other experiments. Thus, color-change takes approximately 3 to 4 hours. Apparently, the earliest stages of the color-change process were not detected in the specimens monitored in holding cages.

To find whether color-change proceeds at different rates at the bases and tips of the arms, BI values for the distal and proximal one-third of the arms were estimated from the series of slides used to study the transition period. From 1630 to 2025 hrs, the mean BI for the arm tips changed from 2.00, to 2.60, 3.93, and 4.47. The mean values for the proximal part of the arms were 1.20, 1.93, 2.90, and 3.63. Evidently, coloration changed at the same time on the proximal and distal parts of the arm. However, the base of the arm always remained more densely pigmented than the tip.

For over 3 days, the arms severed from *O. wendti* and maintained in separate containers changed color at the same time as the whole animals maintained in holding cages (Fig. 2). The arms (and tube feet) still moved in response to mechanical stimulation 4 days after they were removed from brittlestars.

Presumably, they would have lived longer but were discarded at that time. Limited degeneration was observed, with loss of skeletal elements at the proximal ends of several severed arms.

In a preliminary experiment, DAP chips from 5 dark-banded (black) and 5 light-banded (gray) arm segments of *O. wendti* were removed at night. The following morning the chips from dark bands appeared unchanged, having anastomosing chromatophores. However, in the morning the chips from the light arm segments had darkened and their chromatophores, originally punctate, had developed anastomosing processes. The condition of the two sets of DAP chips remained the same the rest of the day.

In a second experiment 10 dark and 10 light DAP chips were removed from banded color-phase brittlestars at night.

Individual chromatophores could not be distinguished in the black DAP chips excised from dark arm segments, but the chromatophores were punctate in gray DAP chips removed from light arm segments. After 2 hours the plates looked the same, but after 19.5 hours (the following afternoon) the black DAP chips were still dark, but the chromatophores of the gray DAP chips (originally punctate) produced anastomoses, and the plates had turned darker brown.

The results were quite different in an experiment using the same number of DAP chips taken from homogeneous color-phase *O. wendti* during the day. At the beginning of the experiment, chromatophores of the DAP chips from light arm segments formed an anastomosing network. The DAPs from dark arm segments also had anastomosing chromatophores, but the cells are so closely spaced, and deeply pigmented, that the borders of individual chromatophores could not be discerned. After 7 hours (at night) the dark plates seemed unchanged, but the chromatophores of DAP chips from light segments were punctate. The appearance of both sets of chips did not change the following day.

The results of these observations on DAP chips may be summarized as follows. The borders of the individual chromatophores were not discernable on the DAP chips from dark arm-bands. They did not exhibit an appreciable day-night change. However, the borders of individual chromatophores from the light regions of the arm were more clearly defined. Due to the changing distribution of chromatophores (probably due to chromatophores migrating deeper within the DAP), and the expansion and regression of anastomosing processes, the DAP chips from light bands turned pale from day to night, and grew darker from night to day. Evidently, the color-change process ceased after a number of hours due to the death of the chromatocytes in the DAP chips.

6. Color-change in response to experimental illumination

Specimens of *O. wendti* were held under continuous light (incandescent illumination) and continuous dark to gauge the influence of illumination on color-change. After 17 hours (at 0900 hrs), the control group had a mean BI of 1.24, the group in the light showed an index of 1.96, and the group in the dark had an index of 2.08. In other words, the brittlestars from both experimental treatments were similar; neither as darkly pigmented as the controls, nor as banded as *O. wendti* at night.

After 30 hours (at 2200 hrs), the control animals were distinctly banded. The BI of controls was 4.16 and the experimental group from the dark had a similar index, 4.00. However, the group held under continuous illumination had an index of 1.50, very similar to the index of animals sampled during the day.

In the short-term experiment carried out at night, the banding index of specimens held in the dark shifted only from 4.04 to 3.84 in 4 hours. The index for animals under incandescent illumination changed from 4.00 to 3.00 during the same period. Controls were not run, but from other observations of *O. wendti* at night, little if any change in the banding index would have been expected during the 4 hour period.

When the experiment was replicated the next day, the BI of animals held in the dark did not change and was 1.25 at 1100 and 1600 hrs. During that 4 hour period, the BI of specimens held under incandescent illumination shifted from 1.20 to 1.00. There was an expected increase in BI for the control group from 1.60 to 2.20, which was expected since the experiment ended late in the afternoon (during the period of color-phase transition).

To examine the short-term effects of artificial illumination on *O. wendti*, banded color-phase brittlestars were held under fluorescent illumination for 1.5 hours. They darkened perceptibly; whereas those held in the dark were unchanged. The same two groups of brittlestars, in the homogeneous color-phase the following morning, were held in the sunlight or in the dark for 1.5 hours, and both groups remained darkly pigmented. In a similar, preliminary experiment, several *O. wendti* and a specimen of the sea urchin, *Diadema antillarum* PHILIPPI, were placed in the dark during the daytime. When examined at 1 and 2 hours later, the brittlestars had not changed color, but the urchin had changed from black to gray.

7. Preference of background color

In 15 experiments, *O. wendti* settled on the black half of the experimental aquarium (n = 10) more often than on the white half (n = 5). However, the difference in the frequency of settlement on black and white backgrounds was not statistically significant (Chi-squared = 1.660 with d.f. = 1; $0.5 > P > 0.1$). Specimens settling on the black background did so somewhat more rapidly ($\bar{x} \pm s = 334.1 \pm 237.59$ sec) than those settling on the white background (413.6 ± 217.61 sec). Yet, the mean times to settle on the white and black backgrounds were not significantly different (t = 0.627, n = 15; $0.9 > P > 0.5$).

8. Reaction to shadow

Ophiocoma wendti moved into a shadow significantly more rapidly in sunlight than in moonlight (t = 4.446, n = 28; $p < 0.001$). Although the same set of specimens responded more quickly to the strong daytime shadows (4.7 ± 1.3 sec, n = 15), the response to shadow also was rapid in moonlight (8.5 ± 2.9 sec, n = 13). Two of the 15 specimens tested in moonlight remained in the unshaded part of the experimental tray, perhaps an indication that the ability to detect shadow, or negative phototaxis, is diminished at night.

9. Sensitivity to illumination

The threshold of response of *O. wendti* arm tips to a graded series of light intensities was tested at 1330 and at 2312 hrs. In the afternoon, animals in the

homogeneous color-phase showed the following numbers of arm tip responses (in parenthesis) to illuminations of the following intensities: 1448.1 mw · cm^{-2} (0), 2082.0 (1), 2838.3 (3), 4185.0 (9), > 4185.0 (17). At night, for brittlestars in the banded color phase, the corresponding figures were 1448.1 mw · cm^{-2} (8), 2082.0 (13), 2838.3 (6), 4185.0 (3), > 4185.0 (0). Thus, the lowest measured threshold for response shifted from 1448.1 mw · cm^{-2} at night to 2082.0 mw · cm^{-2} during the day. Moreover, the hypothesis that figures for the day and night series do not differ in "location" was rejected (KRUSKAL-WALLIS Test: H/D = 9506.902 with d. f. = 1, P < 0.005; see SOKAL & ROHLF, 1969), supporting the conclusion that *O. wendti* responds to lower light levels at night than during the day.

10. Predation on *Ophiocoma* species

Predatory fish attacked *O. pumila* considerably more frequently than they did the other four *Ophiocoma* species. The total numbers of fish attacks registered for each brittlestar species (and, in parentheses, the number of the 12 trials in which attacks occured) were as follows: *O. pumila*, 235 (11); *O. echinata*, 32 (5); *O. wendti*, 27 (4); and *O. paucigranulata*, 21 (4). Specimens of about the same disc diameter were selected for these experiments. For whatever reason, *O. pumila* is particularly succeptible to fish predation.

The fish that attacked *Ophiocoma* were mostly the wrasses *Halichoeres bivittatus* (BLOCH), *H. maculipinna* (MÜLLER & TROSCHEL) and *H. garnotti* (CUVIER & VALENCIENNES). The numbers of fish in the attacking swarms could not be counted accurately. Wrasses (especially small specimens) generally ate only the brittlestars' arm tips, but they could consume entire specimens of *O. pumila*. Attacks of larger fish, *Sparisoma* sp. (parrotfish) and *Gerres cinereus* (WALBAUM) (a mojarra), were infrequent but had a considerable impact. A mojarra, for example, ate a brittlestar in 3 bites. Parrotfish were more apt than wrasses to attack *O. echinata*, *O. paucigranulata* and *O. wendti*.

The contrasting incidence of predation between *O. pumila* and the other species might be due to its overall fragility rather than to any interspecific differences in specialized defensive structures. Although *O. pumila* was attacked more frequently than *O. echinata*, both species have shorter arm spines than *O. paucigranulata* and *O. wendti*. The spines and tube feet of all four *Ophiocoma* species produce mucus, which was demonstrated with live specimens in seawater, using the stain toluidine blue. When mechanically disturbed, all species also exuded a sticky, non-staining mucus which adhered in strands to the arm spines. Specks of reddish-purple staining material were seen in the strings of mucus, but their origin was not determined. It was also noted that the arm spines of all four species, when mechanically disturbed, erect and "lock" in position and then relax, folding against the arm.

Another experiment was performed to compare the camouflage value of the homogeneous and banded color-patterns of *O. wendti*. Banded *O. wendti* were attacked a total of 26 times (2 to 7 attacks on each specimen in 3 min) and the homogeneous color-phase brittlestars were attacked 21 times (0 to 12 attacks per specimen in 3 min). The number of attacks directed towards the banded and the homogeneous color-phase specimens were not significantly different (WIL-

COXON Two-sample Test: $U_s = 24.5$, $n_1 = 6$, $n_2 = 6$, $P > 0.20$; see SOKAL & ROHLF, 1969). The attacking fish (all wrasses) pecked at spines and tube feet rather than nipping off the tips of arms. The results suggest that the fish readily detect both color phases although they did not treat the dead brittlestars as they had the living animals used in the previous predation experiment.

Discussion

1. Background

Prior to this report, a few species of sea urchins were the only echinoderms known to change color. In sea urchins and other invertebrate taxa without eyes, the occurrence, mechanisms, and functions of color-change have been little studied compared with color-change phenomena in groups such as amphibians or fishes (BAGNARA & HADLEY, 1973). Therefore, color-change is an unexpected attribute of brittlestars; and not surprisingly, one which is poorly understood.

Brittlestar coloration has been thought to provide protection from visual predators (HYMAN, 1955), but the slow color-changes described in this report for *Ophiocoma* species could not offer brittlestars the same advantage that flatfish or frogs derive from their rapid color adjustments. In seeking an adaptive explanation for the color-change exhibited by brittlestars, protective crypsis is not ruled out. However, it is notable that in *Ophiocoma* species the color-change activities of the chromatophores which independently respond to light seem to be coordinated with the nervous system's reaction to shadow. Therefore, an explanation of the adaptive significance of integrated color-change and negative phototaxis is developed below.

2. The prevalence of brittlestar color-change

The results show that brittlestars are capable of changing color, and suggest that color-change is an extraocular response to illumination. The four brittlestar species found to change color represent three of the four taxonomically distinct species groups (DEVANEY, 1970) in the genus *Ophiocoma*, indicating that the ability to change color is widespread in the genus. My preliminary observations indicate that *Ophiocoma aethiops* LÜTKEN, collected on the Pacific coast of Panama, changes color much like the Caribbean species, *O. echinata*, which is also in the *aethiops* species group. Many other congeners may change color if the incidence of this attribute in other Pacific *Ophiocoma* species approaches the incidence in Atlantic species. The occurrence of color-change among other *Ophiuroidea* remains to be determined. It would be interesting to find whether brittlestar species named and identified on the basis of their color have the capacity to alter their coloration!

The color-pattern of *O. wendti*, which transforms so markedly from the homogeneous color-phase to the banded color-phase, has generally escaped the attention of taxonomists, even though the two color-phases might have been confused as different taxa. The color-pattern of *Ophiocoma* specimens is fixed at the time they are preserved. Apparently most museum specimens of *O.*

wendti have been collected during the day since the banded color-phase is poorly represented in museum collections. The observations on *Ophiocoma* show that the pigmentation pattern of each brittlestar is unique, although the constituent colors can change. The particular banded color-pattern of each specimen of *O. wendti* and the mottled colors of individual *O. echinata* appear to have a specificity as unmistakable as a fingerprint. The same is probably true for variegate, brightly colored species such as *Ophiothrix fragilis* (ABILDGAARD) and *Ophiopholis aculeata* (RETZIUS). It is possible that other brittlestar species have a greater degree of color variation than currently recognized, if they have an ability to change color.

3. Factors affecting color-change

Ophiocoma wendti maintained in holding cages under natural lighting conditions displays a regular schedule of color-change. Transitions in color-phase are obvious around 0700 and 1800 hrs. A complete change between the homogeneous and banded phases takes 3 to 4 hours. Observations on the schedule of color-change of isolated arms, and of portions of the DAP chips, suggest that the color-change is independent of the central nervous system. Similar conclusions on the independent activity of chromatophores have been drawn from experiments on the response of isolated diadematoid sea urchin chromatophores to light (studies on urchins are reviewed in: MILLOTT, 1975; WEBER, 1983). The chromatophores of *Ophiocoma* species have not been isolated and tested. Therefore, the idea that brittlestar chromatophores act as independent effectors is suggested, but has not been proved. Interestingly, chromatophores in DAP chips live for less than a day, but the severed arms were active and changed color for 4 days, greatly contrasting with the observation of ARSHAVSKY *et al.* (1976 a) that the isolated arms of *Amphipholis kochii* LÜTKEN live only 10 to 20 min.

The diel differences in brittlestar color indicate that color-change is either an endogenous rhythm or that it is engendered by the light regime. The results of short term experiments, comparing *O. wendti* held under constant light and constant dark conditions, show that brittlestars change color in response to light intensity. In two short-term experiments, banded specimens at night darkened when artificially illuminated. In contrast, dark, homogeneous color-phase specimens held in the dark during the day did not become banded. At present there is not a single, simple explanation for the difference of the response of the brittlestar chromatophores between night and day. Perhaps the response takes a longer time during the day or perhaps there is an endogenous control that affects the banding and darkening processes differently, possibly reflecting differing reactions to waxing and waning illumination or the spectral quality of light. There may also be a physiological basis for the contrasting day and night responses which depends on cellular processes associated with chromatophore motility.

In the long-term experiment, the animals held in continuous light and in continuous dark conditions all showed an intermediate BI after 17 hours (during the day). This is neither a clear response to the experimental lighting nor evidence of an endogenous rhythm of color-change. In fact, it is not known

whether the result is an experimental artifact or a product of normal processes. However, after 30 hours (at night) the results were exactly as expected if the coloration were a simple response to the local light regime. That is, animals in the dark for 30 hours were banded and those held in the light were darkly colored. It is clear that coloration can change in response to illumination, but further experiments are required to examine the apparent lack of color-change response during the daytime, and the intermediate BI values found after 17 hours in the long-term experiment. There is only a suggestion, but no proof, that color-change is affected by an endogenous rhythm.

4. Significance of the negative phototaxis

Although the color-change response appears to operate independently of the nervous system, brittlestars have another conspicuous behavioral response to light that directly involves the nervous system, negative phototaxis. *Ophiocoma wendti* quickly moves into shadow in sunlight or moonlight, but its reaction is most rapid and decisive under strong illumination. In addition, the directional movement of *O. wendti* is not affected by the color of the substratum. Thus, the response to shadows appears to be purely a reaction to light intensity. The cryptic behavior of *O. wendti* and other brittlestars is attributable to negative phototaxis and positive stereotaxis (*i. e.*, movement in response to solid surfaces) (ARSHAVSKY *et al.*, 1976 b; this study), although brittlestar scototaxis (detection and movement towards distant dark areas) remains a possibility to be tested (COWLES, 1910).

Negative phototaxis plays an important role in brittlestars' avoidance of predatory fish. The potential impact of exposure to predation was demonstrated in experiments in which all four *Ophiocoma* species were damaged by predacious fish, and *O. pumila* was found to be particularly liable to fish attacks. RANDALL (1967) reports 34 species of shallow-water Caribbean reef fish that prey on brittlestars. Of those, 11 species had stomach contents containing *Ophiocoma* species, and at least 3 fish species in RANDALL's samples had fed on *O. wendti* and 4 species on *O. echinata*.

Five of the species which RANDALL found to feed on *Ophiocoma* are active diurnally, but two feed at night and one feeds both day and night (COLLETTE & TALBOT, 1972). Because brittlestars are subject to predation both day and night, negative phototaxis can be beneficial at all times. Movement towards shadow can conceal brittlestars from visual predators, and because retreat towards shadows often leads brittlestars into crevices, negative phototaxis also helps to insure mechanical protection from attack.

There is experimental evidence indicating that the nocturnal activity of brittlestars (which may involve negative phototaxis) is a predator-avoidance behavior (HENDLER, 1984). The present study suggests why the Caribbean *Ophiocoma* species, which are subject to predation by diurnal wrasses, are active at night, as are several Indo-Pacific congeners (DEVANEY, cited in REESE, 1966). It also suggests why *Ophiocomina nigra* (ABILDGAARD), a related brittlestar which does not change color (FONTAINE, 1962 a, c), and is immune from fish predation (WILSON *et al.*, 1977), is found in dense, epifaunal concentrations during daylight and at night. MAGNUS (1967) reports that *O. scolopendrina*

(LAMARCK), in the intertidal, is active both day and night during low tide. Of course, *O. scolopendrina* in the intertidal may be less liable to predation during low tide than it would be during high tide in the daytime or at night. I would predict that if *O. scolopendrina* changes color, its color phases are correlated with diel cycles rather than tidal cycles, because I hypothesize that color-change functions primarily in photobehavior rather than in crypsis.

5. Brittlestar coloration as camouflage

A brittlestar's coloration may afford some protection from visual predators. The mottled and banded color patterns widespread among *Ophiocoma* species (and seen in many other brittlestars) could provide disruptive camouflage or otherwise interfere with predators' visual processes. Transverse arm-banding could be a particularly effective protective-pattern for brittlestars moving their arms at a speed approximating the critical flicker-fusion frequency (the speed that bands must pass the visual plane to produce the illusion of a unicolored object) of predatory fish (DIENER et al., 1976; McFARLAND & LOEW, 1983). Similar functions for banding patterns have been suggested in snakes (POUGH, 1976). Unfortunately, this hypothesis is presently untestable because the critical variables (speed of arm movement and flicker-fusion response of piscine predators) are not known in sufficient detail. In fact, none of the attractive reasons for suspecting that brittlestars are camouflaged by their color patterns can be readily tested or proved.

Several factors detracted from the reliability of the predation experiment performed to test the camouflage value of the homogeneous and the banded color-phases of *O. wendti*. The crevice-dwelling brittlestars were tested on an exposed sandy bottom, an unnatural background. It would have been interesting to perform these tests during the day and at night, but previous experiments (HENDLER, 1984) indicated that fish preying on brittlestars would not be observed at night. The immobility and any morbid characteristics of the dead animals used in the experiment were drawbacks, but unfortunately during daylight hours only dead banded color-phase animals were available.

Both homogeneous and banded color-phase animals were detected by fish during the day. The relatively reserved response of fish to the dead animals, compared with their vigorous reaction to living brittlestar prey, suggests that immobility of a brittlestar provides some protection against predation (or that dead brittlestars are unattractive to fish). Therefore, the results of the experiment must be interpreted with caution. On the basis of the results the camouflage value of brittlestar coloration cannot be ruled out. However, immobility and concealment may be the more important defensive tactics of *Ophiocoma* species.

6. The significance of color-change

Experiments and speculations concerning diel color-change in diadematoid sea urchins have linked the phenomenon with protection from radiation and with protection from predation. The urchins' transformation from black in the day to gray and black at night is controlled by chromatophores which respond (as

independent effectors) directly to light. This color-change is thought to regulate the intensity of light reaching the photosensitive elements controlling the reflexive movements of the sea urchin's spines, marshalling the defensive spines in the direction of shadows. Unfortunately, the spine movements have not been tested and proved to deter predators. It also has been suggested, but not proved, that densely pigmented areas of the test provide the urchin protection from damaging solar radiation (MILLOTT, 1954, 1968, 1975; YOSHIDA, 1966; GRAS, 1981; GRAS & WEBER, 1983; WEBER, 1983).

The considerable variation in the extent and pattern of banding between individuals of *O. wendti* is a clue that the dark bands do not protect *O. wendti* from solar radiation. Furthermore, FONTAINE's (1962 c) experiments on the sensitivity of *Ophiocomina nigra* to light show that color morphs of a related brittlestar do not suffer significantly different degrees of damage from solar radiation. MILLOTT (1954) suggested that the darkest areas of the test of *Diadema* are associated with particularly photosensitive tissues, but the relatively irregular distribution of dark bands of *O. wendti* suggests that photosensitive tissues must be more uniformly distributed in *O. wendti* than in *Diadema*.

However, in *O. wendti* and *Diadema* there may be a similar coordination of nervous (behavioral) and non-nervous (chromatophore) responses. During the daytime (and under strong light), the chromatophore pigments are dispersed, giving *O. wendti* a homogeneous dark color. At night the pigment cover, especially in the pale-banded portions of the arm, is reduced. Moreover, brittlestars in the banded color-phase at night are more sensitive to light than the same specimens in the homogeneous color-phase tested during the day. At night the photonegative response, in sensitive specimens, is elicited by an estimated light level at least 533.9 mw · cm^{-2} lower than during the day. The exact threshold is not known however, because the action spectrum (sensitivity to different wavelengths) of *O. wendti* was not characterized, and the quality of light probably varied with different illuminator settings. Moreover, the response curve of the lightmeter probably did not match the output of the light source.

Recently, STUBBS (1982) demonstrated activation of the brittlestar radial nerve by light, by recording single unit spikes propagated along the nerve following light-on and light-off stimulation. By testing the exposed nerve cord, in arms with and without skeletal plates, he inferred that photoreceptive tissue is associated with the arm plates, rather than the radial nerve. Thus, brittlestars appear to have a dermal receptor form of extraocular sensitivity (WOLKEN & MOGUS, 1979).

The chromatophores, which cover the superficial portion of the arm plates of *O. wendti* in the homogeneous color-phase may interfere with light reaching the suggested photosensitive tissue within the plates. Presumably, light would have to penetrate the calcareous skeleton and soft tissue, including the opaque chromatophores, before reaching any photoreceptors. The surface of the DAPs has a knobbed texture and the transparent knobs have the convex appearance of lenses. These putative lenses overlay a denser, possibly reflective, region of the skeletal stereom. The dorsoventral alignment of the *c*-axes (the principal optical axis) in the brittlestar arm (RAUP, 1966), would maximize the amount of light penetrating the DAPs. I suspect that the chromatophores, punctate and deep in the DAP in the banded color-phase in dim light, maximize the exposure of light-

sensitive tissues to available light. Furthermore, the knobs are not only covered and uncovered by the expanded and contracted chromatophores, but they appear to be surrounded by a ring of chromatophores below the surface of the arm plate. Therefore, I speculate that light is not only conducted through the knobbed, transparent layer of the skeletal stereom, but perhaps channeled towards presumed photosensitive tissue by the opaque layer of dark chromatophores ringing the calcite "lenses". Perhaps the location of the light receptors may be found by examining the tissue structures at the focus of these putative lenses.

In summary, I suggest that the color-change reaction may influence light reception. It is possible that the animal's sensitivity to light, regulated by chromatophore pigment movement, enables it to distinguish between light and shadow in moonlight as well as in daylight. However, the apparent lack of physiological importance for the bands *per se* (*i. e.*, for energy conservation), suggests that the banded pattern may confer camouflage from visual predators or that it has no evident adaptive value. At night, when the banding pattern is especially pronounced, *O. wendti* tends to be most exposed and vulnerable and would be expected to benefit from disruptive camouflage. Therefore, it is suggested (though not proved) that the dark arm bands camouflage the arms, but that the color-change process (involving chromatophore response in the dark and light portions of the arm and disc) regulates the exposure of photosensitive tissue to light.

Summary

1. Brittlestars of the genus *Ophiocoma* can change color. Color-change in *O. wendti,* and possibly other brittlestars, is effected by the movement of pigments in light-sensitive chromatophores. *O. wendti* undergoes a more striking change in color than *O. echinata, O. paucigranulata,* and *O. pumila,* and it is more sensitive to light than its congeners.

2. Intact specimens of *O. wendti,* as well as severed arms and excised arm plates, have distinctive day and night color-phases. Transformation between phases takes 3 to 4 hours. The color-change is influenced by light, and possibly by a rhythmic, endogenous component.

3. The negative phototaxis of *O. wendti* is elicited by a lower level of illumination at night than during the day. It is suggested that the brittlestar's sensitivity to light may be affected by color-changes that shield photosensitive tissues.

4. Color-change coordinated with negative phototaxis may facilitate the defensive shadow-seeking response under varying illumination levels. Color-change also confers pigmentation patterns which may camouflage brittlestars from predacious fish.

Acknowledgements

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