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An Unusual Bluegreen Alga Symbiotic with Two New Species of *Ulosa (Porifera: Hymeniacidonidae)* from Carrie Bow Cay, Belize*

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With 13 figures and 1 table

Key words: Symbiosis, *Cyanophyta, Porifera,* ultrastructure, pigments, nutrition

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Abstract. Two new species of the sponge genus *Ulosa* were found living in symbiosis with a chroococcacean cyanophyte (cyanobacterium) in shallow Caribbean coral reefs off Belize (Central America). *Ulosa funicularis* is a stringy green sponge (styles: 157 × 2.5 μm, mean dimensions); *U. arenosa* is a thickly encrusting, shaggy, brownish-greenish mottled species with sandy ectosome (styles: 175 × 3.6 μm). The endosymbiotic algae make up 50% of the cellular sponge tissue. The algal cells are light green, spherical, 5–9 μm in diameter, and divide by median constriction. Electron microscopy shows that cell walls are fully developed but that thylakoids are unusual for their inflated sacs, which are in communication with the nucleoplasmic regions. Although the pigment composition is typical for the *Cyanophyta,* the phycobiliproteins occur in considerably

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reduced quantities. Because this alga has a fine structure that differs from other known Chroococcales – including *Prochloron*, a symbiont of didemnid tunicates and possibly a prochlorophyte – its appropriate systematic placement will require comparative evaluation of cytological characteristics in the *Cyanophyta*. Nutrient flow from alga to sponge is evident from electron photomicrographs and autoradiography of labeled compounds.

Problem

Among the many endosymbionts associated with sponges, bacteria and unicellular algae are found to be of substantial ecological advantage for they provide their hosts with an ample food resource (reviews: BRIEN, 1973; SARÀ & VACELET, 1973). Certain bluegreen algae (cyanobacteria, "zoocyanelles") occur abundantly in many shallow-water sponges from well-illuminated habitats in the Mediterranean Sea (SARÀ, 1966) and tropical Atlantic and Indian Oceans (DE LAUBENFELS, 1950; RÜTZLER, in preparation). This association is uncommon among the metazoans, but it was recently found in didemnid ascidians (NEWCOMB & PUGH, 1975). The structure of some of the minute algal symbionts and the details of their interaction with sponge cells were clarified by the application of electron microscopy (SARÀ, 1971; VACELET, 1971; GAINO *et al.*, 1976). Taxonomic problems remain because the validity of ultrastructural characters for identification of unicellular *Cyanophycea* has not yet been demonstrated.

During a study of bacterial and algal symbionts of Caribbean coral reef sponges (RÜTZLER, in preparation), I obtained many results comparable to observations available for Mediterranean species. Among the unusual findings, however, is the close relationship between an unidentified unicellular cyanophyte and cells of two new *Ulosa* species.

Material and Methods

Origin of specimens for systematic study is listed under the species description. Length and maximum width of 25 randomly selected spicules were measured for each. Other light microscope observations were made on hand-ground sections of samples embedded in epoxy resin (RÜTZLER, 1978). The material is deposited in the National Museum of Natural History, Smithsonian Institution.

All material used for histological or experimental work was collected at one patch reef, 0.8 km WSW from Carrie Bow Cay (16 °48′N, 88 °05′W), Belize. Glutaraldehyde fixation (2 % in buffered seawater, four hours at 29 °C) was followed by dehydration and critical point drying (liquid CO_2) for scanning electron microscopy. Osmium tetroxide postfixation (2 % in distilled water, one hour at 20 °C) and subsequent staining of sections with uranyl acetate were employed for transmission electron microscopy (RÜTZLER & RIEGER, 1973).

To demonstrate transfer of photosynthetic products from algal symbionts to sponge tissue, small specimens of the two new *Ulosa* species were incubated *in situ* in 0.5 l clear perspex containers to which 20 µCu/l sodium bicarbonate C^{14} was added. After four hours of exposure, the sponges were returned to their habitat for three hours, then fixed and embedded for electron microscopy. Sections (1 µm thick) were coated with Kodak NTB-2 emulsion and stored in a refrigerator for 20–100 days until development. The position of silver grains relative to algae and sponge cells was verified by phase contrast microscopy.

Results

1. Genus *Ulosa* De Laubenfels, 1936

Hymeniacidonidae with ascending, branching, and interconnected spongin fibers cored by styles. The status of this genus is discussed by Hechtel (1965, p. 51), Pulitzer-Finali (1977, p. 72), and Wiedenmayer (1977, p. 146).

a. Ulosa funicularis, new species (Figs. 1–4)

Description. Thin incrustations supporting clusters of slender anastomosing terete branches (Fig. 1, colour), grayish green color, punctiform surface (Fig. 2 a), soft consistency. Average specimens extend over 100–200 cm^2 area, covering rock, algae (*Valonia* sp.), live coral (*e. g., Millepora* sp., *Acropora cervicornis, Siderastrea* sp.), and other sponges (*Geodia neptuni*). Encrusting portions 1—2 mm thick, branch diameter 1—3 mm. Yellow exudate under adverse conditions in seawater; macerates quickly if left in neutral formalin fixative.

Spongin fibers run longitudinally, cored by 5–15 rows of styles (Fig. 2 b). Peripheral spicules in confusion or subreticulate. Abundance of foreign spicules and sand, and of 5—9 µm unicellular bluegreen algae throughout the tissue (Fig. 3). Oval choanocyte chambers have 40 × 25 µm maximum dimensions. Maturing larvae, 100–160 µm in diameter, occur in specimens fixed during May 1975 and June 1977. Styles slender and straight, with blunt ends slightly set off by constriction and tips pointed gradually, and with distinct axial canals; dimensions: 148–163 µm × 2.4–2.6 µm (range of means); 6 specimens: Table 1, Figs. 4 a, c, d.

Fig. 2. *Ulosa funicularis*. a: Close-up of live specimen showing surface detail. b: Skeleton tracts in section perpendicular to surface.

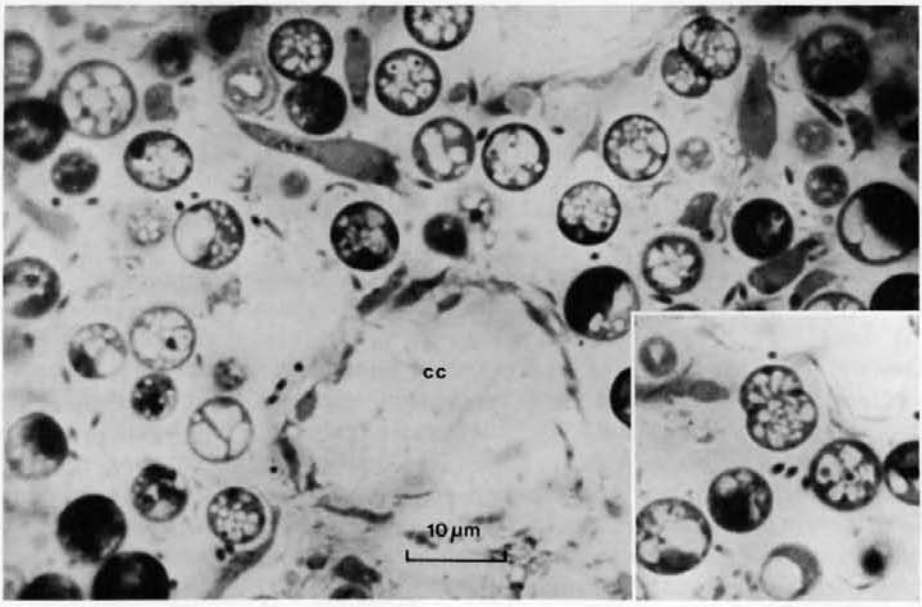

Fig. 3. Symbiotic algae surrounding choanocyte chamber (cc) of *Ulosa funicularis*. Inset: Dividing stage.

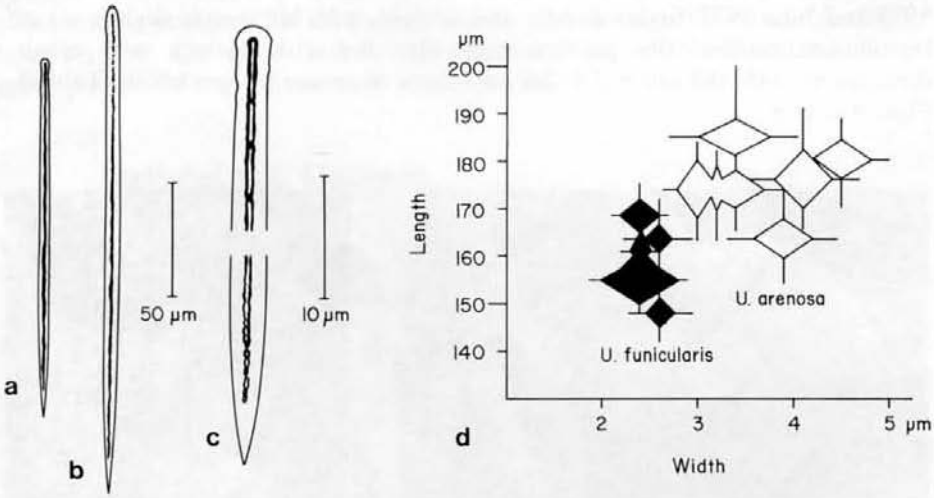

Fig. 4. Comparison of *Ulosa* spicules. a, c: Styles of *U. funicularis*. b. Style of *U. arenosa*. d: Plot of measurements (diamonds: means ± 2 s.e.; bars: ± s.d.). (Data from Table 1).

Remarks. *Ulosa funicularis* differs in colour, shape, and spicule characteristics from all other sponges known in this genus. Symbiosis with the alga appears to be obligate. Antimicrobial metabolites from this species were recently discovered and described (WRATTEN & FAULKER, 1978). The name is derived from Latin *funiculus:* thin rope, string.

Fig. 1. Underwater view of *Ulosa funicularis* growing on another sponge, *Geodia neptuni* (picture width: 18 cm).

Fig. 5. Underwater view of *Ulosa arenosa* (picture width: 9 cm).

Material and distribution. Holotype: USNM 24531; 21 June 1977; lagoon patch reef, 0.8 km due 241 ° (magnetic) from Carrie Bow Cay, Belize; at reef margin near bed of turtle grass *(Thalassia testudinum),* 4 m depth. Paratypes: USNM 24532; 24 May 1975; USNM 24533; 24 May 1976; near type location, 3–4 m depth. USNM 24534; July 1977, J. FAULKNER, col.; near Hat Cay, Lighthouse Reef, Belize; SW fore reef, on edges of turtle grass beds, usually 10–15 cm above sand, 1–2 m depth. Also reported from Glover's Reef, Belize, 2 m (WRATTEN & FAULKNER, 1978). Other material examined: EM 75-B, EM 78-4 (spicules only; from the type locality).

Table 1. Spicule measurements (µm) for specimens of *Ulosa funicularis* and *U. arenosa.* (Data for 25 styles each, unless otherwise noted)

Specimen No.	Length					Width					Remarks
	min.	max.	mean	± s. d.	± s. e.	min.	max.	mean	± s. d.	± s. e.	
					Ulosa funicularis						
USNM 24531	147.5	175.0	157.3	7.9	1.78	1.9	3.2	2.4	0.42	0.10	Holotype
USNM 24532	152.5	180.0	163.5	7.3	1.63	2.4	3.2	2.6	0.35	0.08	
USNM 24533	142.5	180.0	160.8	8.1	1.80	1.9	2.9	2.4	0.21	0.05	
USNM 24534	135.0	175.0	147.9	6.3	1.39	2.4	3.2	2.6	0.34	0.08	
EM 75-B	155.0	167.5	159.5	4.5	1.40	2.1	2.9	2.4	0.27	0.09	n = 10
EM 78-4	140.0	162.5	154.8	7.3	2.53	1.9	3.2	2.4	0.54	0.19	n = 8
Total	135.0	180.0	157.3	5.5	2.24	1.9	3.2	2.5	0.10	0.04	
					Ulosa arenosa						
USNM 24535	165.0	197.5	174.0	10.5	2.35	2.4	3.5	3.2	0.30	0.07	Holotype
USNM 24536	147.5	235.0	185.3	14.6	2.18	2.4	4.8	3.4	0.66	0.10	n = 45
USNM 24537	145.0	177.5	164.3	9.6	2.15	2.4	4.8	3.9	0.62	0.14	
USNM 24538	150.0	187.5	176.0	14.5	3.23	3.2	4.8	4.1	0.61	0.13	
EM 75-C	150.0	195.0	173.8	11.0	2.83	2.4	3.5	3.0	0.35	0.09	n = 10
EM 78-1	170.0	200.0	180.2	9.3	2.08	3.2	4.8	4.5	0.56	0.13	New growth
EM 78-2	160.0	185.0	174.3	8.1	2.10	2.4	4.8	3.4	0.64	0.17	n = 10
Total	145.0	235.0	175.4	6.5	2.44	2.4	4.8	3.6	0.54	0.20	

b. Ulosa arenosa, new species (Figs. 5, 6)

Description. Thickly encrusting, irregularly undulating, some specimens with pronounced ridges and short stubby processes (Fig. 5, colour). Mottled brownish green to bluish green color, shaggy sand encrusted surface without obvious openings, soft consistency. Typical specimens are 2–4 cm thick and cover 100–400 cm² surface on rock; occasionally epizoic on other sponges (*e. g., Geodia neptuni*).

Ectosome heavily impregnated by fine sand grains (10–15 µm particle size), in places forming a continuous cortex, 0.5 mm thick (Fig. 6 a). Foreign particles also dispersed throughout choanosome. Ascending spongin fibers measure 50–80 µm in diameter, cored by 5–20 rows of spicules. Symbiotic algae (Fig. 6 b), yellow exudate, and size of choanocyte chambers identical to *Ulosa funicularis*. No eggs or developing larvae observed. Styles longer and thicker, but otherwise very similar to the preceding species; tips often blunt or tapering

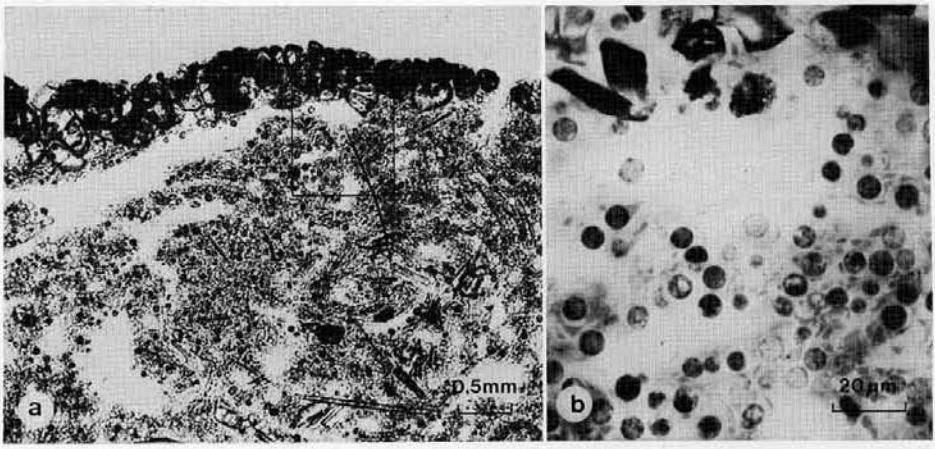

Fig. 6. *Ulosa arenosa.* a. Section perpendicular to surface showing sand cortex and distribution of symbiotic algae. b: Enlarged area marked in a.

with a step; dimensions: 164–185 µm × 3.0–4.5 µm (range of means); 7 specimens: Table 1, Figs. 4b, d.

Remarks. Symbiosis with the same species of alga, skeleton structure, spicule morphology, and abundance of foreign inclusions suggest that *Ulosa arenosa* is closely related to *U. funicularis.* Although both species occur at the same locality, they were never confused in the field as each is morphologically distinct, without transitional stages. On the basis of surface structure and consistency, *U. arenosa* can be mistaken for an encrusting *Dysidea* species; its sand cortex of variable thickness causes the mottled color patterns. Differences in style dimensions in the two species are significant (Table 1, Figure 4). The name of this species is derived from Latin *arenosus:* full of sand.

Material and Distribution. Holotype: USNM 24535; 21 June 1977; lagoon patch reef, 0.8 km due 241° (magnetic) from Carrie Bow Cay, Belize; 4 m depth. Paratypes: USNM 24536; 17 May 1975; USNM 24537 and USNM 24538; 12 May 1978; patch reefs near type location, 3–4 m depth. Other material examined: EM 75-C, EM 78-1, EM 78-2 (spicules only; from the type locality).

2. The algal symbiont

Morphology. The single spherical cells (Figs. 7–9, 10 a) measure 5–9 (6.7 ± 0.18) µm in diameter. Fresh algae under the light microscope show a thin colorless cell wall surrounding light green granular cytoplasm that is broken up by one or several refringent inclusions of varying size. These "spaces" take up 10–80 % of the cell volume and do not accept standard histological stains (Fig. 3). On average, 3–4 % of the cells are in advanced stage of division measuring up to 9 × 7 µm. Cell division (binary fission) takes place by median

constriction after the formation of a low equatorial ridge (Figs. 3, 7 d, e, 10 b, c, 11 b).

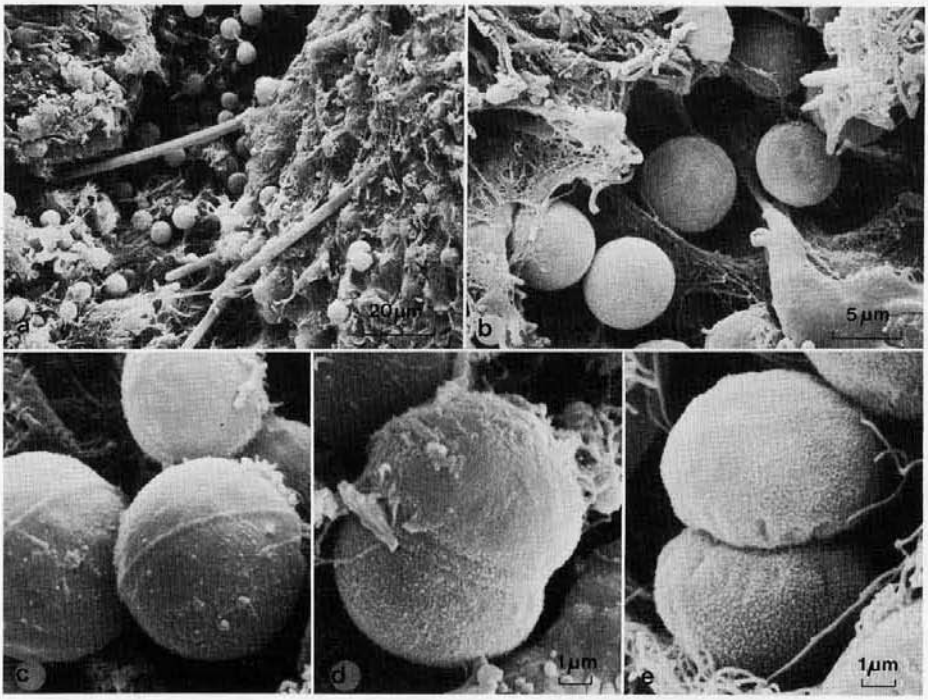

Fig. 7. Scanning electron micrographs of algal symbionts inside *Ulosa funicularis*. a: Tissue and spicules. b: Algae and sponge cells enlarged. c–e: Dividing stages of algal cells.

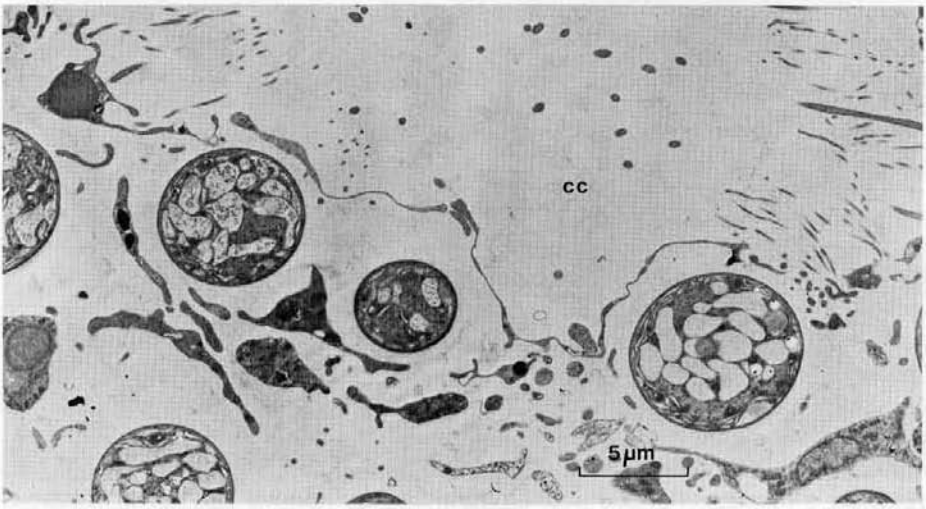

Fig. 8. Transmission electron micrograph of algae in tissue outside choanocyte chamber (cc) of *Ulosa arenosa*.

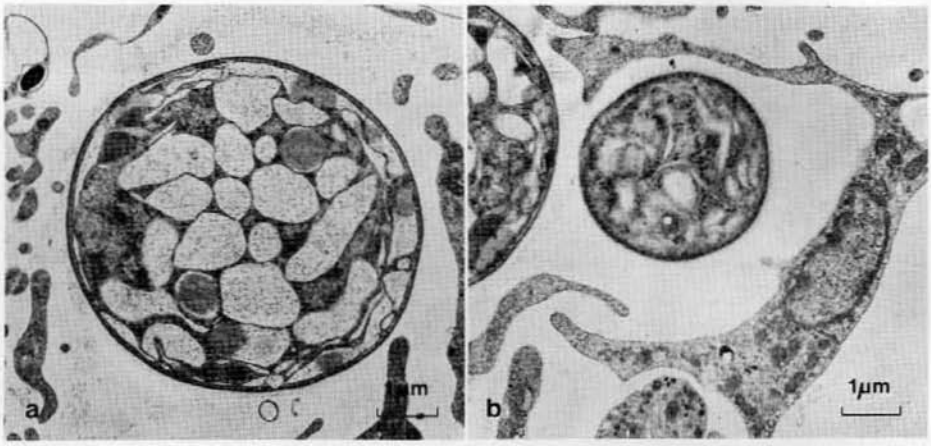

Fig. 9. Algae in *Ulosa arenosa*. a: Median section. b: Tagential section with adjacent sponge cell.

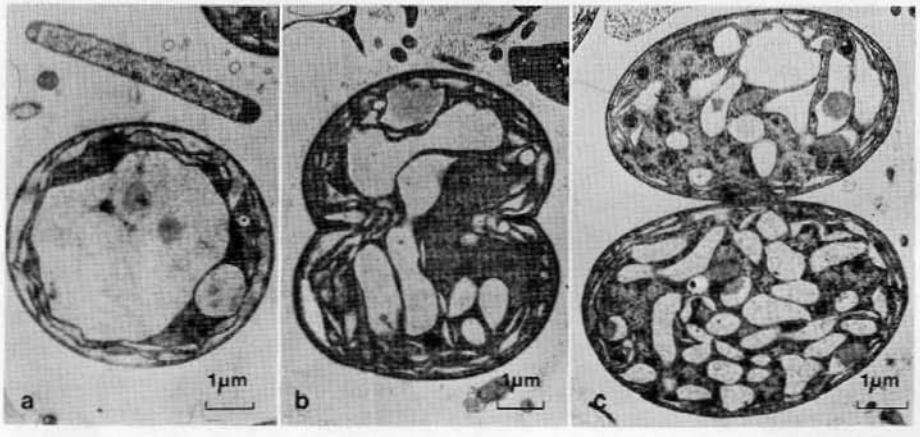

Fig. 10. Algae in *Ulosa arenosa*. a: Cell with large central zone and associated bacterium. b, c: Dividing stages.

Cytology. A normal, typical cell wall (four layers, LI-LIV) that is 34–40 nm thick overlays the cytoplasmic membrane (plasmalemma). The electron dense outer membrane (LIV) is convoluted and coated by a layer of perpendicular sheath fibrils approximately as thick as the cell wall (Fig. 11 a).

The photosynthetic apparatus is unusual for its extreme intrathylakoid vacuolation (Figs. 9, 12). Although most of the wavy membranes run parallel to the cell surface within the peripheral 20 % of the cell radius, perpendicular sacs appear here and there in the sections (Fig. 12). The shortest observed distance between parallel membranes is 10 nm, the average vesicle diameter 60 nm, reaching a maximum of 330 nm. There are no indications that the membranes might originate at the plasmalemma (LANG, 1968). On the other hand, clear connections exist between the thylakoid vesicles and the large presumed nucleo-

plasmic areas (see below), and the same flocculent and granular materials are visible in both (Fig. 12). There is no stacking of thylakoids, of which there are no more than five layers per cross-section, always separated by cytoplasmic intrusions.

Rounded, elongate or irregular electron transparent areas, 2–20 per section, fill the central portion of each algal cell (Figs. 8–10). They measure 0.3–4.0 µm in diameter and are separated from the surrounding cytoplasm by single unit membranes that also connect to the thylakoid vesicles. The only visible structure

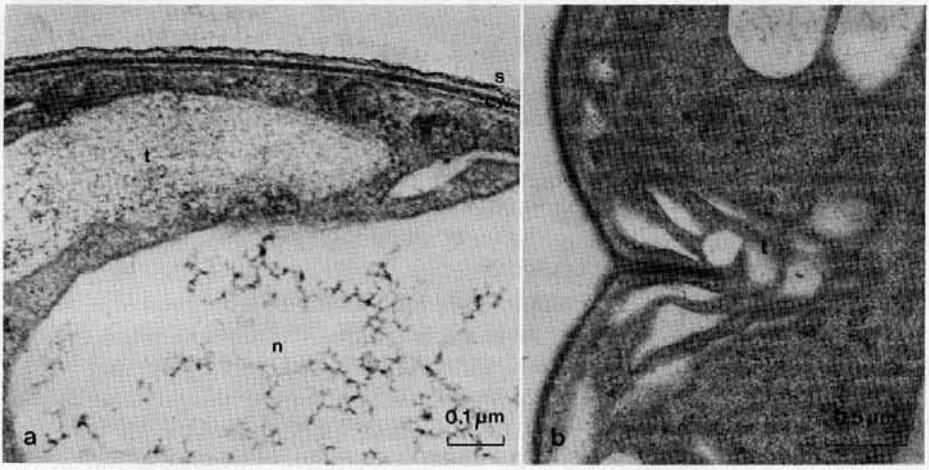

Fig. 11. Enlarged peripheral views of algae in *Ulosa*. a: Cell wall (cw) and sheath (s), thylakoid (t), and nucleoplasm (n), *U. funicularis*. b. Constricting cell wall separating thylakoids (t), *U. arenosa* (detail of Figure 10 b).

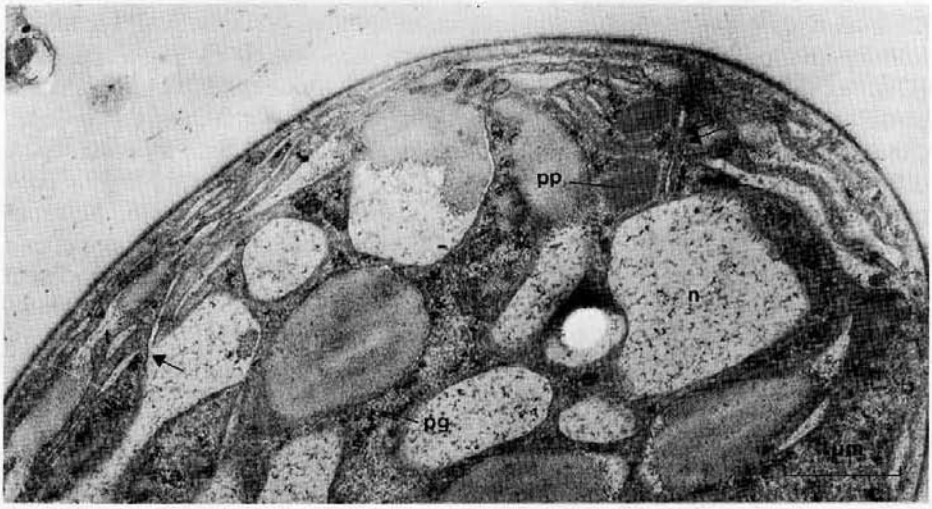

Fig. 12. Enlarged view of peripheral area of alga in *Ulosa arenosa* showing nucleoplasm (n), polyglucoside granules (pg), polyphosphate granules (pp), thylakoid (t), connection thylakoid – nucleoplasm (arrow), and thylakoid sac arranged perpendicular to cell surface (double arrow).

in these zones is a loosely flocculent material, possibly DNA strands, which in some areas seems condensed causing a finely granular appearance (Figs. 9, 11, 12).

Among the identifiable cellular inclusions are polyphosphate granules (polyhedral bodies) 300–500 nm in diameter (Fig. 12). They are located predominantly in the peripheral cytoplasm, up to six per section. Groups of 7–12 nm polyglucoside granules appear throughout the cytoplasm but are particularly evident in the areas around the nucleoplasmic regions. Phycobilisomes, if present, are not detectable with the fixation and staining methods used.

Pigments. An initial survey of pigments failed to reveal phycobiliproteins in an aqueous extract of frozen *Ulosa funicularis*. Thin-layer chromatography (sucrose) of acetone extracts showed the presence of chlorophyll a and β carotene, but not of chlorophyll b (N. WITHERS, pers. comm.). Further study of isolated algal cells indicated that the carotene is located in the sponge protein rather than in the algae, and that small amounts of phycoerythrin and phycocyanin were detectable by absorption and fluorescence spectroscopy (E. GANTT, pers. comm.). Since bilin pigment levels were much lower than usual in bluegreen algae, stimulation of their production was attempted by *in situ* shading. A 125 cm^2 area of *Ulosa arenosa* was covered by a double cone of polaroid foil that reduced the light level to 6 % of ambient intensity. After nine days the sponge showed vigorous new growth inside the cone and was frozen, together with a control from tissue of the same specimen exposed in normal light. Subsequent laboratory analyses were inconclusive as they neither revealed an expected decrease of algal population nor an increase of phycobilin production in the shaded sponge parts.

Taxonomic position. On the basis of the following characteristics, this alga can be classified as a member of the family *Chroococcaceae (Cyanophyta, Chroococcales):* pigmented prokaryotic cells, solitary and spherical; reproduction by division into two equal daughter cells after in-growth of annular wall (DROUET & DAILY, 1965; ROUND, 1965). Generic placement of this species is not possible at present because, on the level of resolution of the light-microscope, closely related similarly simple forms have been shown to have a substantially different fine structure, particularly where the thylakoid morphology is concerned (SARÀ, 1971; LEWIN, 1975; LE CAMPION-ALSUMARD, 1976; SCHULZ-BLADES & LEWIN, 1976; WHATLEY, 1977). Similar problems arose in classifying other, smaller but very common and fine structurally diverse chroococcal sponge symbionts (VACELET, 1971); GAINO *et al.*, 1976; RÜTZLER, in preparation). An evaluation of cytological characters as resolved by electron microscopy for systematic revision will be needed before further classification can be attempted.

3. Sponge-Alga interactions

In the material examined, the algal symbionts are evenly distributed throughout the host tissue. Basal regions of the choanosome as much as 10 mm away from

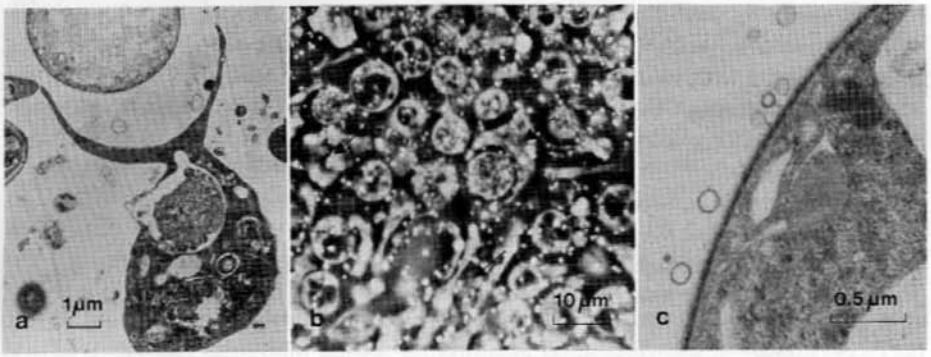

Fig. 13. Sponge-alga interaction. a: Sponge engulfing and digesting algae. b: Autoradiograph, phase contrast, showing silver grains over algae and sponge cells (arrows). c: Droplets exuded from cell wall of stressed alga.

the closest sponge surface are as densely populated as ectosomal areas. Point counts (300 random points per specimen) from 1 µm sections show that 48–52 % of the cellular material is composed of algal cells. Even new sponge growth under artifically lowered light levels (6 % of normal) contains algae in the same density as occur elsewhere, and with the same or even slightly raised percentage (4 %) of dividing stages. Algal cells are situated in the sponge mesohyl within the meshwork of collencytes (Figs. 7a, b, 8, 9b) and do not cause any tissue reaction in their host. Phagocytosis by archeocytes occurs only now and then; of several hundred algae viewed, only three were found engulfed or partly digested (Figs. 13a, b).

Light microscope autoradiographs of specimens of both *Ulosa* species incubated *in situ* with C^{14} show strong activity in the animal cells. In the absence of detectable phagocytosis, this activity demonstrates transfer of dissolved assimilation products from alga to sponge (Fig. 13b). Tissue from a similar six-hour experiment prepared for electron microscopy shows algal cells emitting 80–140 nm droplets (Fig. 13c). This condition, however, may be attributable to a slight yellow exudate in the incubation water and may not be an indication of normal translocation of algal materials. The droplets were not seen in freshly fixed material.

Discussion

With a size range of 5–9 µm, the *Ulosa* symbionts approach that of the dinoflagellate symbionts (7–10 µm) known from clionid sponges in the Mediterranean (Sarà & Liaci, 1964; Crameyrolles-Duclaux, 1970) and Caribbean Seas (Pang, 1973; Rützler, 1974). Among the cyanelles, only *Aphanocapsa raspaigellae* (6–12 µm) from the sponge *Ircinia variabilis* (Feldmann, 1933; Sarà, 1971) and *Prochloron* species (7–15 µm) from didemnid ascidians (Lewin, 1975; Newcomb & Pugh, 1975) are of similar size, shape and mode of reproduction.

In addition to containing a considerable amount of bilin pigments, *Aphanocapsa raspaigellae* (Feldmann, 1933), differs from the unidentified alga

of this study by lacking a sheath, by showing conventional thylakoids with parallel, closely spaced membranes, and by causing the mesohyl of the host sponge to form lacunar spaces around the symbiont (SARÀ, 1971). *Prochloron* has an unusual pigment composition for a prokaryote as it seems to lack phycobilins entirely and contains chlorophyll b in addition to chlorophyll a (LEWIN & WITHERS, 1975; THORNE *et al.*, 1977). This alga is therefore considered a prochlorophyte (LEWIN, 1976). Like *A. raspaigellae, Prochloron* lacks an external sheath and the peripheral thylakoids are flattened, even stacked in some areas (WHATLEY, 1977).

More comparative study and experimental work will be needed to explain the curious thylakoid development in the *Ulosa* symbiont. According to the review by LANG (1968), intrathylakoidal vacuolation occurs mainly in aged cells and in heterocysts, both examples that cannot serve as explanation in the present context. Reduced light level by endosymbiosis in sponges has been shown to have a different effect on thylakoids. Small chroococcal symbionts in *Verongia* and *Chondrilla* have spiralled thylakoids that increase the number of turns with distance of the alga from the sponge surface (VACELET, 1971; GAINO *et al.*, 1976). A comparable light gradient does not exist inside *Ulosa,* and both species, with their stringy or convoluted encrusting growth mode, may have adapted to the light requirements of the symbionts.

The function of the large central electron transparent areas remains undetermined. A comparable central zone separated from the cytoplasm and different from the nucleoplasm of most bluegreen algae was described from *Prochloron* and tentatively classified as either nucleoplasm or a primitive type of vacuole (WHATLEY, 1977). Another peculiarity of the *Ulosa* symbiont is the position of polyphosphate granules near the cell periphery where, on the other hand, polyglucoside grains are lacking or are reduced in number.

The four-layered cell wall is unmodified in all metazoan cyanelles studied. Nutrient flow from algae to sponge cells takes place by phagocytosis and, possibly, by absorption of exuded materials (SARÀ, 1971; VACELET, 1971). Since cellular digestion of symbionts in *Ulosa* seems to be rare, soluble organic materials are likely to be responsible for the demonstrated transfer of photosynthates, a process known from many associations between invertebrates and dinoflagellate symbionts (TAYLOR, 1974).

Summary

Ulosa funicularis and *U. arenosa* are new species of hymeniacidonid *Demospongea* that are common on some shallow (1–4 m) patch reefs in the western Caribbean Sea. Both sponges live in symbiosis with an unidentified species of chroococcal bluegreen algae, or cyanobacteria. The algae occur intercellularly throughout the sponge body and make up half of the total tissue volume. With an average size of 7 µm this plant is among the largest single-cell algal endosymbionts, comparable to eukaryotic "zooxanthellae", and prokaryotic *Aphanocapsa raspaigellae* and *Prochloron* species. Pigment composition is typical for a cyanophyte but thylakoid fine structure is different from that known in other cyanelles. Neither sponge cell arrangement nor algal cell wall

structure show reactions to the symbiotic habit. Nutrient transfer from alga to sponge is accomplished predominantly by means of dissolved assimilation products rather than by phagocytosis of whole cells, thus being comparable to the mechanism known from similar symbioses with dinoflagellates.

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Note added in proof: The alga described here is close to, or possibly identical with *Synechocystis trididemni* LAFARGUE & DUCLAUX (Ann. Inst. océanogr., Paris, 1979, 55: 181), a species of which the description had not yet been published when I presented my paper (see footnote, p. 1). I regret not having been able to discuss my findings with G. DUCLAUX at the occasion of the Paris Colloquium.